

Impacts of Fire on Bats in the Central Appalachians

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## **Abstract (academic)**

Fire occurrence was widespread in the central Appalachians pre-European settlement due to Native American ignition and occasional lightning strikes, and continued through European settlement. During this time, low to mixed severity burns supported a suite of ecological communities that were fire adapted. In the mid-20<sup>th</sup> century, the frequency and intensity of fire decreased regionally, resulting in profound forest composition shifts. Land managers now are prioritizing prescribed fire as a restoration tool in current and transitioning fire dependent communities. However, it is unclear how the re-introduction of fire will affect bat community assemblages, particularly after the severe White-nose Syndrome related population declines of many cave-hibernating bat species. To address this concern we used acoustic detectors to sample bat activity levels in burned and unburned environments to examine habitat and temporal effects of fire on bat species in a repeatedly burned landscape on the northwestern portion of the George Washington National Forest. We found evidence for weak positive fire effects on the northern long-eared bat, Indiana bat, little brown bat, big brown bat/silver-haired bat group, high frequency phonic group, and total bat activity. Temporal effects of fire were only apparent for the big brown bat, where we observed a negative relationship between activity and time since fire. Additionally, historic wildfires may offer a suitable surrogate to assess long-term burn impacts on bats, which in turn can be used to better inform bat and prescribed fire relationships. To examine effects of historic fire on bats, we assessed bat presence using acoustic detections at 16 paired burned and unburned forest stands in Shenandoah National Park. Overall, we found few or mostly equivocal relationships of bat occupancy across species relative to burn condition or time since fire at SNP, indicating there is little evidence to support the concept that fire has a significant ecological effect on bats in this portion of the central Appalachians. Riparian areas

are particularly important for bats, and serve as foraging and drinking areas, roost sites, and travel corridors. Because fire impacts dry upland and mesic riparian areas differently, it is possible that fire will impact bats differently in burned and riparian habitats. To examine fire effects on bats in riparian and upland habitats, we used paired sampling to monitor bat activity in burned, unburned, riparian, and non-riparian areas. Burn and riparian variables had empirical support to explain activity of all bat species. However, coefficients for these species were small and confidence intervals overlapped zero indicating that differences between habitat configurations were marginal. Our results suggest bats have somewhat species-specific responses to fire that differ between upland and riparian habitats, but that large landscape level prescribed fire has a slightly positive to neutral impact on all bats species identified at our study site post-fire suppression.

## **Abstract (public)**

Fire occurrence was widespread in the central Appalachians pre-European settlement from to Native American ignition and occasional lightning strikes, and anthropogenic burning continued through European settlement. During this time, burns supported many ecological communities that were fire adapted, i.e., oak (*Quercus* spp) and pine (*Pinus* spp)-dominated types. In the mid-20th century, fire decreased regionally, resulting in changes to forest composition. Land managers now are prioritizing prescribed fire as a tool to restore or re-establish fire dependent communities. However, it is unclear how the re-introduction of fire will affect bats, particularly after the severe White-nose Syndrome related population declines of many bat species. To address this concern, I used acoustic detectors to measure bat activity levels in burned and unburned landscapes to examine habitat and temporal effects of fire on bat species in a repeatedly burned landscape on the northwestern portion of the George Washington National Forest. I found evidence for weak positive fire effects on the northern long-eared bat, Indiana bat, little brown bat, big brown bat/silver-haired bat group, high frequency phonic group, and total bat activity. Temporal effects of fire were only apparent for the big brown bat, where we observed decreasing activity as time since fire increased. Because riparian areas are particularly important for bats in the region as foraging and drinking areas, roost sites, and travel corridors, I also focally compared burned and unburned riparian areas. Burn and riparian variables had support to explain activity of all bat species, however differences between habitat types were marginal. My results suggest bats have somewhat species-specific responses to fire that differ between upland and riparian habitats, but that large landscape level prescribed fire has a slightly positive to neutral impact on all bats species identified at our study site post-fire suppression. Lastly, examining effects of historic wildfires may allow managers to infer long-

term burn impacts not yet observable with current prescribed burning. To examine effects of historic fire on bats, I assessed bat presence using acoustic detections at paired burned and unburned forest stands in Shenandoah National Park. Overall, I found few relationships of bat occupancy across species relative to burn condition or time since fire, indicating that fire likely does not have a significant ecological effect on bats in this portion of the central Appalachians.

## **Dedication**

This work is dedicated to my parents, Bill and Victoria Austin, my brothers, Will and Ben Austin, and my fiancé, Michael Muthersbaugh, for their unwavering support and love in all things big and small.

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## **Chapter 1: Bat Activity Following Repeated Prescribed Fire in the Central Appalachians**

### *Abstract*

To restore and manage fire-adapted forest communities, land managers are now prioritizing use of prescribed fire. However, it is unclear how the re-introduction of fire will affect bat community assemblages, particularly after the severe White-nose Syndrome related population declines of many cave-hibernating bat species. To address this concern we monitored and compared bat activity in burned and unburned habitat across a temporal gradient. We found evidence for slightly positive fire effects on the northern long-eared bat, Indiana bat, little brown bat, big brown bat/silver-haired bat group, high frequency bats combined, and total activity. We observed temporal effects only for the big brown bat, with a negative relationship between activity and time since fire.

### *Introduction*

Fire occurrence was widespread in the eastern United States pre-European settlement due to Native American ignition and occasional lightning strikes (Nowacki and Abrams, 2008), and resulted in a number of fire-adapted forests. As a result of the fire suppression era beginning in the 1920's, the frequency and intensity of fire decreased through the 1960's in the Mid-Atlantic Highlands of Virginia, resulting in profound forest composition shifts that favor fire-intolerant species (Abrams, 1992; Yarnell, 1998). Through "mesophication" (Nowacki and Abrams, 2008), shade-intolerant and fire-dependent species fail to regenerate and self-replace as competing shade-tolerant and fire-intolerant species begin capturing canopy or light gaps in the forest stand (Kreye et al., 2013). These alterations result in an alternative stable forest condition whereby



shading promotes cool, damp microclimates and the production of non-flammable fuels. As mesophication progresses, it becomes increasingly difficult to reverse, and forests may be locked into a steady mesophytic state wherein only shade-tolerant, fire-intolerant plant species are maintained (Nowacki and Abrams, 2008). With increased concerns over the impacts of mesophication on forest ecosystems, land managers are prioritizing prescribed fire as a tool for maintaining current and transitioning fire-dependent communities in the East (Hessl et al., 2011; USDA Forest Service, 2006). Impacts of fire on bats are largely unknown (Carter et al., 2000) despite protection of multiple bat species under Endangered Species Act.

Throughout North America, including the central Appalachians, bats currently are of conservation concern (Carter et al., 2000; Perry, 2012), due to the impacts of White-nose Syndrome (WNS; Francel et al., 2012; Reynolds et al., 2016) and the development of wind energy (Arnett and Baerwald, 2013; Erickson et al., 2016). Among the diverse suite of bat species present in the central Appalachians is the endangered Indiana bat (*Myotis sodalis*; MYSO) and the threatened northern long-eared bat (*Myotis septentrionalis*; MYSE), two species potentially impacted by active forest management, including prescribed fire (Carter et al., 2000; Ford et al., 2016b; Perry, 2012; Silvis et al., 2016b). Because there has been limited work examining the relationships of these and other bat species in the central Appalachians relative to the return of fire as a prescriptive tool, land managers are often challenged to show that burning is not additive in negative impacts to these stressed species (Ford et al., 2016a; Johnson et al., 2010b).

Research on the short-term effects of fire on bats suggest that bats display species-specific responses to fire-modified vegetation (Austin et al., 2017a; Cox et al., 2016; Owen et al., 2004), with larger-bodied bats benefiting from clutter reduction that simplifies flight (Aldridge and Brigham, 1988; Norberg and Rayner, 1985)(Aldridge and Brigham, 1988; Norberg and

Rayner, 1985). Snags in burned areas may be of higher quality because the newly-created canopy gaps allow for increased canopy light penetration that aids in thermoregulation and expedites juvenile bat development (Boyles and Aubrey, 2006; Johnson et al., 2009; Zahn, 1999). Bats may even be robust to some roost tree loss (Silvis et al., 2015), as may result from fire. Additionally, newly-created roosts may offset loss (Ford et al., 2016a) and remaining trees are likely more conducive to roosting due to fire-modified cavity and bark conditions (Perry, 2012). However, Reilly et al. (2016) found that repeated prescribed fire in the southeastern Piedmont changed composition and structure of trees in the midstory but not in the overstory, indicating that foliage roosting species may be less affected by fire. Many insect taxa, including Lepidoptera, that serve as prey for bats, also benefit from prescribed fire and associated increases in nectar-producing plants (Rudolph and Ely, 2000) as well as new growth that provides a substrate on which to lay eggs (Evans et al., 2013).

Acoustic surveys have been used to monitor fire effects on bat activity. Cox et al. (2016) found that bat activity in the Cumberland Plateau was higher after spring and fall prescribed burns in savannahs than after spring and fall prescribed burns in woodlands. Loeb and Waldrop (2008) and Silvis et al. (2016a) found thinning and burning treatments yielded higher total bat activity than control stands. However, there has been relatively limited research on the effect of repeated prescribed fire relative to bats, such as that used for restoration and maintenance of fire-dependent communities, on bats in the central and southern Appalachians. In the Chicago metropolitan area, repeated prescribed fire had a positive effect on bat activity (Smith and Gehrt, 2010), and in a longleaf pine (*Pinus palustris*)-wiregrass (*Aristida stricta*) ecosystem in Florida higher bat activity was associated with sites that experienced short fire-return intervals (Armitage and Ober, 2012). Furthermore, much of the research in the central Appalachians has examined

repeated prescribed fire effects on bat roosting habitat (Ford et al., 2016a; Johnson et al., 2009, 2010b), leaving a need for research on the effects of repeated prescribed fire on bat foraging habitat.

With the continued spread of WNS, the severe population declines of many cave-dwelling species of bats, the endangered status of MYSO and the threatened status of MYSE, understanding of how forest management practices such as prescribed fire affect bats is critical. Regionally in the central Appalachians, managers will be challenged to show that burn programs designed to benefit other natural resource components will also benefit bats or, at minimum, will not exacerbate population reductions from WNS (Ford et al., 2016a). To investigate this, we compared bat activity in burned and unburned habitat and examined edge effects associated with burning. Previous research in the central Appalachians found strong species-specific responses to forest habitat characteristics (Ford et al., 2005); thus, we predicted that bats would have species-specific responses to repeated prescribed fire and the resulting fire-modified habitat and vegetation characteristics as well. For example, larger-bodied and less maneuverable bats (Barclay, 1985; Norberg and Rayner, 1985) should respond differently to burned and unburned habitat with higher activity in burned habitat due to reduced vegetative clutter (Loeb and Waldrop, 2008; Silvis et al., 2016a). Conversely, smaller-bodied bats (*Myotis* spp. and the tricolored bat; *Perimyotis subflavus*; PESU) as well as the eastern red bat (*Lasiurus borealis*; LABO) should display neutral responses to repeated prescribed fire and resulting fire-reduced vegetative clutter (Austin et al., 2017a).

## *Methods*

### *Study Area*

We conducted our study on the 3,751-hectare Warm Springs Mountain Preserve (WSM) and portions of the George Washington National Forest (GWNF) that is cooperatively managed, in terms of fire, by the United States Forest Service (USFS) and The Nature Conservancy (TNC). The area is within the western Ridge and Valley portion of the central Appalachian Highlands. Depending on elevation and aspect, forests are predominately comprised of pine-oak (*Pinus* spp.) mixtures of white oak (*Quercus alba*), chestnut oak (*Quercus prinus*), northern red oak (*Quercus rubra*), pitch pine (*Pinus rigida*) and table mountain pine (*Pinus pungens*), with blueberries (*Vaccinium* spp.) and bear oak (*Quercus illicifolia*) in the understory. In fire-suppressed areas, forests also contain red maple (*Acer rubrum*) and eastern white pine (*Pinus strobus*; Nowacki and Abrams, 2008) with mountain laurel (*Kalmia latifolia*) in the understory. Elevation ranges from 500 to 1100 meters above mean sea level. In our study area, the USFS and TNC typically use prescribed fire in March and April of each year with aerial ignition (M. Smith, TNC, pers. comm.). The matrix of variously-aged burned plots (ranging in age from <1 to 8 years and frequency from 1 to 3 burns) and unburned plots provides a diversity of habitats (Figure 1-1). The conservation goals of TNC include preservation of biodiversity, control of invasive plant species, and restoration of historic fire regimes in fire-dependent pine and oak forests (M. Smith, TNC, pers. comm.).

### *Data Collection*

We recorded bat activity using acoustic detectors (Songmeter ZC; Wildlife Acoustics, Maynard, Massachusetts, United States <sup>1</sup>) with SMM-U1 microphones from 24 May through 2

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<sup>1</sup> The use of any trade, product or firm names does not imply endorsement by the US government.

August 2015. We programmed acoustic detectors to record data from 2000 to 0700 hours. We sampled burned and unburned sites equally using transects that extended 180 meters perpendicularly into each management unit. Transects were 360 m long and contained seven acoustic detectors set 80 m apart, with the center detector placed at the interface of the burned and unburned habitat. (Figure 1-1). We spaced detectors 80 meters apart to avoid detection of a single bat on two detectors simultaneously and to ensure relative independence in measurements among detectors. Edge sites were nearly always near unimproved forest roads that served as compartment fire breaks on the area. Our objective was to sample individual locations within a transect for five nights, however our true sampling duration fell between one and nine nights.

We used generalized random tessellation stratified sampling (GRTS) to spatially balance transect locations (Philippi, 2013). Following the protocol of Ford et al. (2005), we collected call data, site location, canopy closure, and basal area at the detector site. We derived elevation, aspect, and slope using digital elevation models within ArcMap 10.2.2® software (ESRI, Redlands, California, United States) available online through USGS (<http://data.geocomm.com/dem>), and burn history using burn layers provided by TNC.

### *Data Analysis*

*Bat Call Identification.* We identified calls using Kaleidoscope version 4.1.0, classifier version 3.1.0 at the sensitive setting (Wildlife Acoustics, Maynard, Massachusetts, United States). We used the default signal parameters in Kaleidoscope (8-120 KHz frequency range, 500 maximum inter-syllable gap, 2 minimum number of pulses, enhance with advanced signal processing) and specified nine individual species that are known to occur within our study region: big brown bats (*Eptesicus fuscus*; EPFU), hoary bats (*Lasiurus cinereus*; LACI), LABO, silver-haired bats (*Lasionycterus noctivagans*; LANO), MYSE, MYSO, little brown bats (*Myotis*

*lucifugus*; MYLU), eastern small-footed bats (*Myotis leibii*; MYLE), and tricolored bats. We had validated ~ 50% of calls to insure reliability of automated identification.

*Fire Effects.* We created a set of fourteen *a priori* negative binomial mixed models that incorporated burn and habitat variables to assess their effects on bat activity level as well as nested random effects for site and transect to account for the nested nature of sites within transects and nights within sites (Table 1-1). We compared models representing competing hypotheses using an information theoretic approach by ranking models using Akaike's Information Criterion corrected for overdispersion and small sample size (QAICc; Burnham and Anderson, 2002). We identified a confidence set of models within  $\Delta QAICc < 2$  as competing models. To account for uncertainty in the model selection process we used package MuMIn (Barton, 2016) in program R to obtain full model averaged estimates, unconditional standard errors, and 95% confidence intervals to assess individual variable effects on bat activity levels (Grueber et al., 2011; Symonds and Moussalli, 2011).

## *Results*

We collected data on 707 detector nights at 149 sites (21 transects) for up to nine nights at each site. Uneven sampling periods among sites occurred due to periodic detector failures from low batteries or black bear (*Ursus americanus*) damage. When visually examining calls, we identified a systematic error where insect noise was classified both as hoary bat and eastern red bat calls. To address for this issue, we visually examined all calls identified by Kaleidoscope using AnalookW v. 3.9f (Titley Electronics, Ballina, NWS, Australia) and removed erroneously-identified insect noise. After removing noise, we re-ran calls through Kaleidoscope to obtain corrected nightly counts of bat calls by species. Kaleidoscope identified 24,180 total call files,

post visual noise removal, and assigned them to nine unique species: EPFU (10,039), LABO (2,665), LACI (795), MYLE (414), MYLU (3,066), MYSE (1,045), MYSO (3,036), and PESU (284). An unusually high number of LANO calls were documented. In Virginia, this species typically is caught only in May as it migrates through the state (Cryan, 2003), though anecdotal reports of greater summer captures have been occurring (M. St. Germain, Virginia Tech Conservation Management Institute, pers. comm.). It is possible that many LANO calls are actually misclassified EPFU calls (Betts, 1998; Ford, 2014), thus we combined all EPFU and LANO calls into one group and refer to them as EPFU/LANO. We also present results for all high frequency bats (*Myotis* spp. and PESU) combined to account for program identification uncertainty among *Myotis* species, and all species combined to examine fire and habitat effects on overall bat activity (O’Keefe et al., 2013, 2014).

Burn condition and elevation were the most important variables for explaining activity levels of EPFU/LANO, MYLU, MYSE, MYSO, high frequency bats, and total activity (Figure 1-2) and had a positive effect on all species (Table 1-2; Table 1-3); the confidence interval for model-averaged burned habitat overlapped zero indicating a neutral/ marginal effect of burned habitat on EPFU/LANO, LABO, MYLU, MYSO, and total bat activity. Five models describing LABO activity were competing, and contained combinations of burn condition, canopy cover, elevation, and basal area (Table 1-3). Model-averaged confidence intervals overlapped zero for burned habitat, elevation, canopy cover and basal area. Edge habitat positively affected LACI activity. The elevation model and the canopy cover model were the top models for LACI with canopy cover having a negative effect on activity and elevation having a slightly positive effect on activity. Confidence intervals for both variables overlapped zero. There were seven

competing models that described PESU activity, with the top model being the null (Table 1-4). We were unable to analyze burn and habitat effects on MYLE due to model convergence error.

### *Discussion*

We found evidence for fire effects on MYSE, MYSO, MYLU, EPFU/LANO, high frequency bats combined, and total activity. For all species and species groups, activity was the highest in edge habitat and slightly higher in burned than unburned habitat. It is likely that larger bodied bats, such as EPFU and LANO, benefit from recent fires due to clutter reduction because it facilitates flight (Aldridge and Brigham, 1988; Brooks and Ford, 2005; Norberg and Rayner, 1985). Hutchinson et al. (2005) found that multiple fires were required over the course of eight years to achieve statistically significant differences in basal area of midstory trees and reductions in basal sprouting. This suggests that multiple years of prescribed burning would be required before long-term benefits to larger-bodied bat species are evident (Austin et al., 2017a). Previous research in the central Appalachians (Austin et al., 2017a), as well as in South Carolina (Ford et al., 2006; Hein et al., 2009) and Mexico (Estrada, 2001) has found that bat activity is high in corridors because they allow for efficient flight for bats; it seems likely that this is also occurs on WSM in and along the roads serving as fire breaks. Similar to riparian corridors (Rogers et al., 2006), the creation of fire breaks may benefit bats by providing efficient travel pathways connecting roosting and foraging areas. These areas of concentrated bat activity may offer potential monitoring locations.

Both MYLU and MYSO displayed slight positive to neutral. These species, while considered more clutter-adapted than LABO and less clutter-tolerant than MYSE (Broders et al., 2004, 2006; Brooks and Ford, 2005), are likely tolerant of a wide range of conditions. Indeed,



Brooks and Ford (2005) noted that MYLU was present across all habitat types in New England. In southern Illinois (Carter and Feldhamer, 2005) and the agriculture landscape of central Ohio (Kniowski and Gehrt, 2014), MYSO utilized bottomland habitat, an area likely unaffected by fire, for roosting and/or foraging.

The clutter-adapted MYSE displayed a positive response to prescribed fire. Immediate effects of a single fire, post-suppression include mortality of understory vegetation and small trees (though dependent on fire severity and slope position), and prolific basal sprouting shortly post-fire (Elliott et al., 1999). In the absence of midstory clutter, basal sprouts may provide additional substrate off which to glean insects (Ratcliffe and Dawson, 2003). Indeed, Silvis et al. (2016a) found that *Myotis* were positively related to low-strata vegetative clutter. Several studies also have documented positive fire-effects on MYSE roosting habitat (Ford et al., 2016a; Johnson et al., 2009; Lacki et al., 2009). In all burn conditions activity had a slightly positive relationship with elevation. This is in contrast with previous research (Ford et al., 2005), but could be a result of the increased energy demands required to achieve lift (Adams et al., 2012; MacAyeal et al., 2011). Also, burn intensity is greater on upper slopes (Mladenoff and Baker, 1999), so reductions in clutter may be more apparent in these locations.

Both competing models describing LACI activity included canopy cover and elevation. These models indicated that activity is negatively related to canopy cover and positively related to elevation. Previous research has found that LACI use rapid, straight flight and long-range echolocation to pursue prey in open habitats (Barclay, 1985). Similar to our findings, Ford et al. (2005) also documented a positive relationship between LACI activity and minimum canopy gap width. Elevation had a slightly positive relationship with LACI activity. However the relationship is weak and why this trend might occur is unclear.

There was lack of support for connection between most burn/habitat variables and LABO activity with the exception of edge habitat. In the central Appalachians, LABO tend to be habitat generalists (Austin et al., 2017b; Ford et al., 2005; Hutchinson and Lacki, 1999). Ford et al. (2005) documented a positive trend with minimum canopy gap size for LABO. Similarly, LABO in our study area utilized the gravel roads present at our edge sites, which served as long linear canopy openings (Austin et al., 2017a; Estrada, 2001; Ford et al., 2006; Hein et al., 2009).

Seven models describing PESU activity were competing models, though the best supported model was the the null. Given the number of competing models, and weight of the null, we found little evidence to suggest that fire has an effect on PESU. Due to prohibitively low sample sizes, we were unable to analyze effects of burn and habitat variables for PESU and MYLU. Small sample sizes for these species may be a result of WNS-related population declines (Ford et al., 2011; Franci et al., 2012; Frick et al., 2010; Silvis et al., 2016b).

Fire is used for conservation of fire-dependent, oak-dominant communities and to promote the montane pine systems, as well as to help land managers meet other stewardship goals (i.e., preservation of biodiversity and control of invasive plant species). Impacts of repeated prescribed fire on bats still are relatively unclear, despite potential effects on listed bat species. Current understanding of a repeatedly burned landscape on bat foraging habitat is limited to the Cumberland Plateau (Cox et al., 2016), the longleaf pine Sandhills (Armitage and Ober, 2012), and urban habitats (Smith and Gehrt, 2010). Our research helps to elucidate effects of repeated prescribed fire in the central Appalachians. Overall, we generally found weak positive to neutral effects of fire on bats environment. Based on burn layers provided by the U.S. Forest Service, WSM, the GWNF directly adjacent to WSM, and Hidden Valley have a higher rate of prescribed fire both spatially and temporally compared to the GWNF overall. Indeed,

despite prioritization of prescribed burning regionally (Brose et al. 2011), it is still a small percentage of public lands overall (S. Croy, USDA Forest Service, pers comm). The lack of negative response from bats to fire at WSM where there is a conglomerate of repeatedly burned stands, suggests that areas where fire is used less frequently would have even less impact on bats. Therefore, bat species, particularly listed species, should not be an impediment for burn programs on the central Appalachian landscape. While it is widely accepted that higher acoustic activity indicates better habitat conditions (Coleman et al., 2014a; Johnson et al., 2010a), understanding the relationship between bat activity levels and foraging habitat suitability merits additional research.

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## **Chapter 2: Effects of historic wildfire and prescribed fire on site occupancy of bats in Shenandoah National Park, Virginia, USA**

### *Abstract*

Given high likelihood of extinction or regional extirpation of several once-common bat species, it is critical that impacts of forest management activities such as prescribed fire on bats be understood so as to minimize potentially additive negative effects relative to the stressor of White Nose Syndrome. Historic wildfires may offer a suitable surrogate to assess long-term burn impacts on bats thus better potential long-term effects of prescribed fire on bats. To examine effects of historic fire on bats, we sampled bat activity at 16 sites that had paired burned and unburned forest stands in Shenandoah National Park in the summer of 2015. There was limited evidence of positive fire effects over time on hoary bats and big brown bats. Overall, we found few or mostly equivocal relationships of bat occupancy across species relative to burn condition or time since fire at SNP. Our results indicate that fire does not have a significant long-term ecological effect on bats in the central Appalachians.

### *Introduction*

Fire suppression efforts in the early half of the 20<sup>th</sup> century have resulted in profound shifts in composition of forests in eastern North America (Abrams, 1992). In the absence of fire, advance regeneration of oaks (*Quercus* spp.) have been outcompeted by shade-tolerant species such as red maple (*Acer rubrum*). This has resulted in dense, shade-tolerant understories and midstories and the eventual failure of oaks to reach the overstory either following harvesting or in gap-phase dynamic processes in Appalachian forests (Abrams, 1992; Brose et al., 2011;



Signell et al., 2005). As such, prescribed fire is increasingly being used to maintain and restore fire-dependent communities, particularly to benefit oaks (Block et al., 2016; Hessburg et al., 2016; Hessler et al., 2011; Iverson et al., 2017; Strahan et al., 2015; USDA Forest Service, 2006). However it generally is unknown how fire impacts wildlife after years of suppression in these systems or how long those impacts to wildlife, either positive or negative persist (Ford et al., 2010; Keyser and Ford, 2006; Perry, 2012).

Regionally, bats currently are of particular conservation concern (Ingersoll et al., 2013) due to extreme population declines of many cave-dwelling species as a result of White-nose Syndrome (WNS; Franch et al., 2012; Frick et al., 2010) and migratory species as a result of wind energy development (Arnett et al., 2008; Arnett and Baerwald, 2013; Erickson et al., 2016). Given high likelihood of extinction or regional extirpation of several once-common bat species (Frick et al., 2010; Thogmartin et al., 2013), it is critical that impacts of forest management activities such as prescribed fire on bats be understood so as to minimize potentially additive negative effects relative to the stressor of WNS. Although prescribed fire is used as a positive stewardship tool to accomplish an array of different forest management objectives (e.g. fuels reduction, oak regeneration, savanna creation; (Abrams, 1992; Nowacki and Abrams, 2008; Peterson and Reich, 2001), because several bat species are protected under Endangered Species Act, fire use faces regulatory restriction due to “take” on bats. Potential negative impacts of fire on bats include direct mortality from smoke inhalation, flame immolation, habitat and roost loss, or disruption of group dynamics (Boyles and Aubrey, 2006; Carter et al., 2000; Dickinson et al., 2010; Guelta, 2005; Perry and McDaniel, 2015). Conversely, fire may benefit bats through clutter reduction that facilitates flight, snag/roost creation, and increased insect prey abundance (Ford et al., 2016a; Loeb and Waldrop, 2008; Perry, 2012; Silvis et al., 2016a).

Throughout the East, pre-WNS research on bat communities has found species-specific responses to prescribed fire, but notably, overall bat activity often is higher in burned than unburned areas (Armitage and Ober, 2012; Cox et al., 2016; Ford et al., 2006; Loeb and Waldrop, 2008; Silvis et al., 2016a; Smith and Gehrt, 2010). Bat species-specific habitat selection is related to size and wing shape (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1985), and studies have documented differences in likelihood of species presence relative to forest vegetation structure (Adams et al., 2009; Müller et al., 2013; Plank et al., 2012), as well as that structural clutter is more influential than prey abundance in determining bat habitat use (Cox et al., 2016). It seems likely, then, that prescribed fire benefits bat communities in the short-term through reductions in structural clutter that improves foraging efficiency (Grindal and Brigham, 1998; Jackson, 2004; Müller et al., 2013; Titchenell et al., 2011) particularly for larger bodied bats such as the big brown bat and the hoary bat (Loeb and Waldrop, 2008; Silvis et al., 2016a). Nonetheless, in the Appalachians and Ozarks for some larger-bodied species, the probability of occurrence and/or activity levels does not differ between burned and unburned forests, i.e., the eastern red bat (*Lasiurus borealis*; (Silvis et al., 2016a; Starbuck et al., 2015), possibly because it has been documented as a habitat generalist in these regions (Ford et al., 2005; Hutchinson and Lacki, 1999). The northern long-eared (*Myotis septentrionalis*) and Indiana bats (*Myotis sodalis*) are of particular conservation concern due to protection under Endangered Species Act.

Although foraging behavior of northern long-eared and Indiana bats , both smaller bats more adapted to cluttered environments, has been found to differ immediately pre- and post-fire in the Appalachians (Dickinson et al., 2009; Lacki et al., 2009), foraging behavior returns to pre-burn patterns within one week (Dickinson et al., 2009). Likewise, Indiana bat home range size (Lacki et al., 2009) and northern long-eared bat (Johnson et al., 2009) and Indiana bat (Johnson

et al., 2010b) roost switching frequency did not change in response to prescribed burning, suggesting that roost availability likely is comparable between burned and unburned areas. In a direct assessment of long-term potential roost availability following prescribed fire, Ford et al. (2016) found that availability of trees with characteristics suitable for northern long-eared bat roosting (e.g., cavities and loose bark) did not change post-fire, although tree species composition of the available pool of suitable roosts changed over time. Furthermore, roost trees in burned areas may be more suitable for bats than those in unburned areas due to overall increased solar exposure resulting from canopy dieback of neighboring trees, allowing for increased light penetration that aids in thermoregulation and expedites juvenile development (Boyles and Aubrey, 2006; Johnson et al., 2009; Zahn, 1999). Collectively, these studies suggest that northern long-eared and Indiana bats may be unaffected by or display a neutral response to fire in the Appalachians. Though the northern long-eared bat and the Indiana bat are of particular concern due to listing, many bat species are currently in decline (Arnett and Baerwald, 2013; Erickson et al., 2016; Francl et al., 2012; Reynolds et al., 2016) and may be further impacted by prescribed fire.

Although these studies provide general insights into how fire may affect bats immediately post-burn and a few years thereafter, very little is known about long-term effects of fire on bats in the eastern U.S. generally or the Appalachians specifically, or the effects relative to WNS-impacted bat populations and communities. These topics have important implications both for long-term forest management plans and conservation of federally threatened and endangered bats. While there are increasing amounts of prescribed burning regionally (Brose et al. 2011), in reality it is a small percentage of public lands overall (S. Croy, USDA Forest Service, pers comm), and the limited history of prescribed fire use precludes assessment of long-

term impacts of fire. Historic wildfires may offer a suitable surrogate to assess long-term burn impacts on bats, which in turn can be used to better inform bat and prescribed fire relationships. Determining long-term use patterns of burned stands by bats will better allow managers to create burn regimens that support bats while also accomplishing forest management goals. Our objectives, therefore, were to assess patterns of site occupancy by bat species among variously-aged burned stands and unburned stands in the central Appalachians. We hypothesized that probability of occurrence would differ between paired burned and unburned stands, with higher occupancy in burned stands than unburned stands due to reduced clutter that facilitates flight and increased insect prey abundance. Furthermore, we hypothesized that probability of occurrence would decrease with increasing burn age, as forest structural clutter increases.

## *Methods*

### *Study Area*

We conducted our study at Shenandoah National Park (SNP). Shenandoah National Park encompasses 79,900 hectares within the Blue Ridge province of the central Appalachian Highlands and spans eight Virginia counties: Warren, Page, Rockingham, Augusta, Rappahannock, Madison, Greene, and Albemarle. Elevation ranges from 171 to 1235 m above sea-level. Previous inventorying and monitoring efforts by Young et al. (2009) identified 35 unique vegetation community types that in part can be attributed to SNP's disturbance history of previous forest harvesting, grazing, and burning prior to park acquisition. Plant communities vary based on aspect and elevation, with northwest facing slopes harboring more chestnut oak and red oak forests with some montane basswood (*Tilia americana*) and white ash (*Fraxinus americana*) found in circum-neutral to basic boulderfield. High elevation (>900 m), ridge top

forests are primarily comprised of stunted chestnut oak (*Quercus montana*), yellow birch (*Betula alleghaniensis*), and northern red oak (*Quercus rubra*; Berg and Moore, 1941; Teetor, 1988), with shrublands, comprised of mountain laurel (*Kalmia latifolia*), black huckleberry (*Gaylussacia baccata*), and *Vaccinium* spp. dominating cliffs and emergent rock outcrops. Low to mid-elevation (roughly 300-900 m) sheltered coves are typically dominated or co-dominated by sugar maple (*Acer saccharum*), but can also contain tulip poplar (*Liriodendron tulipifera*), white pine (*Pinus strobus*), eastern hemlock (*Tsuga canadensis*), and mixed hardwoods depending on elevation and site fertility. The southeast facing slopes are often more varied also consisting of cove and woodland species. Dry to moderately mesic forests typically comprised of chestnut oak, northern red oak, white oak (*Quercus alba*), pignut hickory (*Carya glabra*), and *Vaccinium* spp. dominate northwest facing slopes; white pine is occasionally found at valley bottoms. Pine – oak/ heath woodlands, consisting of table mountain pine (*Pinus pungens*), pitch pine (*Pinus rigida*), and chestnut oak, are located on the most xeric and infertile soils of steep, highly solar exposed mid-slopes. Riparian areas dominated by eastern hemlock, white pine with rosebay rhododendron (*Rhododendron maximum*) understories are limited in extent, making up less than 2% of the park.

Shenandoah National Park has been managed by the National Park Service since 1935. Though SNP occasionally used prescribed fire to enhance public safety and to maintain overlooks and meadows, as well as for exotic plant control, largely there has been no landscape-level application of prescribed fire in the park (R. Gubler, National Park Service, pers comm) as has occurred over the past decade in the adjacent George Washington National Forest (S. Croy, USDA Forest Service, pers comm). The majority of historic fires in SNP were accidental wildfires ignited by lightning strikes, park guests or arson. Wildfire size ranges from

approximately 2 to 7000 hectares, with fires greater >40 hectares occurring nearly every five years since 1933 and nearly every year in past five years. Approximately 24,010 ha have burned between 1933 and 2014 (~30% of total SNP area; Missy Forder, SNP Fire Ecologist, pers. comm.). Time since wildfire at SNP ranged from 3 to 95 years and burn size ranged from 20 to 9,322 hectares (Figure 1-1).

### *Data Collection*

We collected acoustic data from 11 June until 15 August of 2015 during the summer maternity season for bats, enabling us to investigate habitat associations in relation to fire, when bats are most abundant on the SNP landscape and distributed throughout the park (Caceres and Barclay, 2000; Ford et al., 2011; Whitaker and Rissler, 1992). We sampled bat activity at 16 sites that had paired burned and unburned forest stands. We identified logistically practicable and accessible areas in SNP and distributed transects in these areas using generalized random tessellation stratified sampling (GRTS), which allows for monitoring in areas of interest (i.e., burn habitat) while maintaining approximate spatial-balance (Philippi, 2013; Figure 2-1). Transects contained three acoustic detectors (Songmeter ZC; Wildlife Acoustics, Maynard, Massachusetts, United States<sup>2</sup>) at 160-meter intervals, with one deployed at the burned/unburned boundary, and one each in the burned and unburned habitat (Figure 2-2), for a total of 48 detector locations. We prioritized areas that had a burned and unburned interface to minimize landscape effects and enable us to attribute bat occupancy differences to habitat and burn variables of interest. However due to a limited number of accessible burn/unburned interfaces, five sites fell entirely within burned habitat and an additional three transects fell entirely within

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<sup>2</sup> The use of any trade, product or firm names does not imply endorsement by the U.S. government.

unburned units. We programmed acoustic detectors to record data from 2000 to 0700 hours and collected data for 11 days at each site between 11 June and 15 August 2015.

Following the protocol of Ford et al. (2005) we collected call data, site location, canopy closure, and distance to nearest tree in each cardinal direction at each survey site. The point-centered quarter method was used to calculate tree density from distance to nearest tree ultimately providing information on stand structure (Mitchell, 2010). We derived elevation (m), aspect, and slope (degrees) using digital elevation models available online through USGS (<http://data.geocomm.com/dem/>), and burn history from Shenandoah National Park management records. We sine-transformed aspect following the protocol of Garst (2007). We obtained data for weather covariates that may impact detectability of bats (i.e., temperature, wind speed, humidity, and precipitation) from the Meteorological Terminal Aviation Routine (METAR) from digital records (<https://www.wunderground.com/>) from the nearest airport to each detector site.

### *Data Analyses*

*Bat Call Identification.* We identified calls using both Kaleidoscope version 4.1.0, classifier version 3.1.0 at the sensitive setting (Wildlife Acoustics, Maynard, Massachusetts, United States) and Echoclass version 3.1 using species set 2 (Eric Britzke, U.S. Army Engineer Research and Development Center, Vicksburg, Mississippi, United States). Both programs are USFWS approved software versions (<https://www.fws.gov/midwest/endangered/mammals/inba/surveys/inbaAcousticSoftware.html>). We visually examined calls from 16 of 24 randomly selected transects (>50% of calls) identified to species in AnalookW v. 3.9f (Titley Electronics, Ballina, NWS, Australia<sup>3</sup>) to confirm that there were no major classification errors (i.e., classification of noise and insect calls as bats).

*Fire history effects.* Because bat calls are not perfectly identifiable by software (Ford, 2014; Russo and Voigt, 2016) or by hand (Jennings et al., 2008), acoustic data are highly likely to include false positive determinations of species presence, in addition to false negatives. Repeated site surveys result in site-specific capture histories representing detections and non-detections of a species (MacKenzie et al., 2002). Directly modeling detections and non-detections accounts for instances whereby a species is present at the site but was not detected, thus more accurately accounting for presence (MacKenzie et al., 2006). Although standard occupancy models are designed to deal with false negatives, they do not permit false positive detections of presence (Clement et al., 2014; Miller et al., 2011; Royle and Link, 2006). To address this issue, MacKenzie et al. (MacKenzie et al., 2002) developed an approach that allows for imperfect detection. Accordingly, to account for this uncertainty in bat presence, we modeled bat presence in relation to site characteristics and burn history using false-positive occupancy models in program R version 3.2.3 (R. Development Core Team, 2014) using package Unmarked (Fiske and Chandler, 2011).

We created false-positive detection histories for each species by comparing site-night presence determinations from Echoclass and Kaleidoscope; we considered bats to be present under each identification software if the maximum-likelihood value for presence was  $\leq 0.05$ . Because we did not have a “certain” method to determine true presence, we considered agreement in site-night presence between the programs to represent “true” detection/non-detections, and disagreement to represent “uncertain” detections. Understanding the strengths and weaknesses of available automatic identification software is critical in making appropriate decisions for study design, program selection, and interpretation of results in other settings. Given that no acoustic classifier is completely accurate, outcomes from all programs may be



regarded as biased. Likewise, because classifier algorithms vary among programs, it can be reasonably assumed that each exhibits a different bias. Use of multiple identification algorithms therefore helped us identify and protect against bias and possible limitations of individual identification packages.

Because we were interested in assessing effects of burn age and condition while also accounting for other habitat condition effects that could influence bat presence, we compared a series of *a priori* models representing hypotheses about bat foraging habitat selection based on previous research (Table 2-1A, B, C; Table 2-2; Ford et al., 2005; Kaiser and O’Keefe, 2015). For each species, we compared hypotheses using a two-step *information theoretic* approach, wherein we ranked candidate detection and false-positive models using Akaike’s Information Criterion corrected for small sample size (AICc) and then used the best supported combination in occupancy models of interest, also ranked using AICc (Burnham and Anderson, 2002). Due to limited sample size, we restricted models to no more than five covariates. We centered and scaled all covariates before analyses. To account for uncertainty in the model selection process, we identified a confidence set of models within  $\Delta\text{AICc} < 2$  as competing models, then used model averaged estimates, unconditional standard errors, and 95% confidence intervals to assess individual variable effects on probability of occurrence for each bat species of interest (Grueber et al., 2011; Symonds and Moussalli, 2011).

For each species/group, we assessed a list of six detection models, seven false-positive models, and 11 state models. State models contained combinations of the following covariates: aspect, slope, elevation, canopy cover, tree density, burn year, and burn condition (Table 2-1C). Detection models included factors that may have influenced microphone performance (i.e., wind speed and precipitation) and factors that could obstruct a call from being recorded (i.e., canopy

cover and tree density). False-positive models contained variables that may influence call quality (Broders et al., 2004; Clement et al., 2014) as well as presence of species with similar call structures (Britzke et al., 2011; Russo and Voigt, 2016). Species with similar call structure (for example, the Indiana bat versus the little brown bat), can be difficult to distinguish and thus have a higher probability of misidentification and false-positive detection rate.

## *Results*

We surveyed 71 sites (34 burned; 17 edge; 21 unburned) for up to 11 nights in 2015. Uneven sampling periods among sites were due to periodic detector failures such as black bear (*Ursus americanus*) damage or battery failure. Kaleidoscope identified 53,880 call files and detected 9 unique species. Echoclass identified 22,799 call files and also detected 9 unique species. Calls identified by both programs as silver-haired bats (*Lasionycteris noctivagans*) were excluded from analyses due to high uncertainty in automated program identification for this species (Ford 2014). When visually examining calls, we found a systemic error whereby large quantities of insect noise was consistently being classified as hoary bat (*Lasiurus cinereus*) calls. To account for this issue, we visually examined all calls identified as hoary bats by Kaleidoscope using AnalookW v. 3.9f (Titley Electronics, Ballina, NWS, Australia) and removed all erroneously-identified insect noise. After removing noise, we re-ran calls through Kaleidoscope to obtain corrected maximum likelihood estimates. We present results of standard occupancy models for the hoary bat. Detection histories for false-positive covariates (such as little brown bat presence) were generated such that if either program identified the little brown bat as present then it was assumed present.

### *False-positive Occupancy Models*

*Big brown bat (Eptesicus fuscus).* Kaleidoscope and Echoclass results agreed that big brown bats were detected at 17 of 71 sites, providing a “certain” naïve occupancy of 0.24. Either program (but not both) designated big brown bats at an additional 36 sites, giving a possible naïve occupancy of 0.51 (Table 2-3). Two models were competing and contained combinations of burn condition, years since burn, tree density, and the presence of hoary bats, that had empirical support to describe occupancy, detection, and false-positive detection (Table 2-4). Burn condition and an interaction between burn condition and years since burn were the competing covariates for occupancy (Figure 2-3A, B). The competing covariates for explaining detection and false-positive detection were tree density and presence of hoary bats, respectively. Confidence intervals for burn condition and the interaction between burn condition and years since burn overlapped zero and coefficients were small (Table 2-5). Tree density had a positive effect on detection (Figure 2-3C) and the presence of hoary bats had a positive effect on false-positive detection on big brown bats.

*Eastern red bat.* Kaleidoscope and Echoclass results agreed that eastern red bats were detected at 20 of 71 sites, providing a “certain” naïve occupancy of 0.28 (Table 2-3). Either program (but not both) designated eastern red bats at an additional 49 sites, giving a possible naïve occupancy of 0.69. Two models were competing, one of which was the null. The other best-supported model contained slope, wind speed, and presence of little brown bats describing occupancy, detection, and false-positive detection, respectively (Table 2-4). Confidence intervals for slope overlapped zero and estimates were small (Table 2-5). Wind speed had a slightly negative effect on detection (Figure 2-4). The estimate and unconditional standard error for the

presence of little brown bats were large, but had a positive effect on false-positive detection of eastern red bats.

*Hoary bat.* Kaleidoscope detected hoary bats at 40 of 71 sites, providing a naïve occupancy of 0.56 (Table 2-3). There were four competing models containing combinations of an interaction between burn condition and elevation, tree density, wind speed, temperature, and canopy cover that had empirical support to describe occupancy and detection (Table 2-4). The interaction between burn condition and elevation and tree density were the most important covariates for explaining occupancy (Figure 2-5; Table 2-5). Wind speed, temperature, and canopy cover were the most important covariates for explaining detection. Confidence intervals for all state and detection variables overlapped zero and coefficients were small.

*Eastern small-footed bat (Myotis leibii).* Kaleidoscope and Echoclass were in agreement that eastern small-footed bats were detected at 1 of 71 sites, providing a “certain” naïve occupancy of 0.01 (Table 2-3). Either program (but not both) designated eastern small-footed bats at an additional 28 sites, giving a possible naïve occupancy of 0.39. There was one competing model which consisted of slope, mean temperature, and little brown bat presence that had empirical support to described occupancy, detection, and false-positive detection, respectively (Table 2-4). Slope had a negative relationship with occupancy (Figure 2-6A). Temperature had a positive relationship with detection (Figure 2-6B) and the presence of little brown bats had a positive relationship with false-positive detection of eastern small-footed bats (Table 2-6).

*Little brown bat (Myotis lucifugus).* Kaleidoscope and Echoclass were in agreement that little brown bats were detected at 1 of 71 sites, providing a “certain” naïve occupancy of 0.01 (Table 2-3). Either program (but not both) designated little brown bats at an additional 36 sites,

giving a possible naïve occupancy of 0.51. There was one competing model which consisted of an interaction between slope and burn condition, tree density, and northern long-eared bat presence that had empirical support to described occupancy, detection, and false-positive detection, respectively (Figure 2-7A; Table 2-4). Confidence intervals for all state estimates overlapped zero (Table 2-6). Tree density had a positive relationship with detection (Figure 2-7B) and the presence of northern long-eared bats had a positive relationship with false-positive detection of little brown bats.

*Northern long-eared bat.* Kaleidoscope and Echoclass were in agreement that northern long-eared bats were detected at 15 of 71 sites, providing a “certain” naïve occupancy of 0.21 (Table 2-3). Either program (but not both) designated northern long-eared bats at an additional 37 sites, giving a possible naïve occupancy of 0.52. There were three competing models containing combinations of slope, tree density, precipitation, and presence of little brown bats that had empirical support to describe occupancy, detection, and false positive detection (Table 2-4). Slope was the only competing covariate for occupancy. Tree density and binary precipitation were the competing covariates for detection. The presence of little brown bats was the competing covariate for false positive detection. Slope had a negative relationship with occupancy (Figure 2-8). Confidence intervals for tree density and binary precipitation overlapped zero and coefficients were small (Table 2-5). With other covariates set at mean value, the presence of little brown bats had a strong, positive relationship with the probability of false-positive detections of northern long-eared bats.

*Indiana bat.* Kaleidoscope and Echoclass were in agreement that Indiana bats were detected at 7 of 71 sites, providing a “certain” naïve occupancy of 0.10 (Table 2-3). Either program (but not both) designated Indiana bats at an additional 31 sites, giving a possible naïve

occupancy of 0.44. There were six competing models, one of which was a null, containing combinations of slope, aspect, elevation, burn condition, canopy cover and presence of little brown bats that had empirical support to describe occupancy, detection, and false positive detection (Table 2-4). Slope, aspect, elevation, burn condition, and an interaction between burn condition and aspect were the competing covariates for estimating occupancy. Confidence intervals for all state covariates overlapped zero and coefficients were small (Table 2-5). The competing covariates for explaining detection and false-positive detection were canopy cover and presence of little brown bats, respectively; both had a positive relationship with the presence of Indiana bats (Figure 2-9).

*Tricolored bat (Perimyotis subflavus)*. Kaleidoscope and Echoclass were in agreement that tricolored bats were detected at 4 of 71 sites, providing a “certain” naïve occupancy of 0.06 (Table 2-3). Either program (but not both) designated tricolored bats at an additional 29 sites, giving a possible naïve occupancy of 0.41. There was one competing model which consisted of slope, tree density, and little brown bat presence that had empirical support to describe occupancy, detection, and false-positive detection, respectively (Table 2-4). The confidence interval for slope overlapped zero and the estimate was small (Table 2-6). Tree density had a positive relationship with detection (Figure 2-10) and the presence of little brown bats had a positive relationship with false-positive detection of tricolored bats.

## *Discussion*

We found few or mostly equivocal relationships of bat occupancy across species relative to burn condition or time since fire at SNP, indicating there is little evidence to support the concept that fire has a significant ecological effect on bats in this portion of the central

Appalachians. There was limited evidence of positive fire effects over time on hoary bats and big brown bats. Big brown bat and hoary bat wing morphology supports flight in relatively uncluttered habitats (Barclay, 1985; Menzel et al., 2002; Norberg and Rayner, 1985) as would occur more post-fire in SNP forests than in unburned stands. Our data follow this trend, albeit weakly. Big brown bat occupancy in burned areas was negatively related to years since burn attributable to the highest amount fire-reduced clutter immediately post-burn thereby facilitating flight and ease of foraging. Although big brown bats are considered habitat generalists (Owen et al., 2004), they readily utilize more open habitat, including that resulting from prescribed fire and forest thinning treatments in the Appalachians (Loeb and Waldrop, 2008; Silvis et al., 2016a).

In absolute terms, occupancy was lowest in unburned habitat, intermediate in burned habitat, and highest in edge habitat for the big brown bat and the Indiana bat. Edge sites were nearly always low-traffic, gravel roads, which serve as fire breaks in SNP but also provide linear corridor habitats for bats with some overstory and a completely open mid- and understory. Previous studies (Estrada, 2001; Ford et al., 2006; Hein et al., 2009) have found that bat activity is high in corridors such as these, that invariably serve as efficient travel pathways for bats; it seems likely that this is also the case in SNP. Roads also provide uncluttered foraging space with “sides” that provide additional surface area from which bats can glean and hawk insects (Faure et al., 1993; Ratcliffe and Dawson, 2003).

Hoary bat and little brown bat occupancy in each burn condition was dependent on elevation and slope, respectively. However the relationship is weak and why this trend might occur is unclear. Little brown bat occupancy in all burn conditions had a negative relationship with slope. In edge and burned habitat, occupancy decreased steadily with increasing slope, but quickly dropped to zero in unburned habitat where slope exceeded 10 degrees. Several studies

have found that little brown bats in the mountains are strongly associated with second order streams (Ford et al., 2005; Johnson et al., 2010a; Schirmacher et al., 2007). Jachowski et al. (2014) found variable effects of slope among species in northwestern New York but the confidence intervals overlapped zero, indicating that the trends were negligible. Although slope had a small effect size for little brown bat occupancy, it nonetheless was included in our confidence set of models, and had a marginally negative to negative relationship with occupancy of all *Myotis* species, the tricolored bat, and the eastern red bat. Collectively, this suggests slope has a neutral to marginally negative impact on likelihood of presence of these bat species in the central Appalachians.

Slope was the only important covariate for explaining occupancy for all species where burn condition did not have an effect (eastern red bat, eastern small-footed bat, northern long-eared bat, and tricolored bat), and it was negatively related to individual species presence. Our results could be a function of prey locality. In the evening, cold-air drainage (Whiteman, 2000) potentially forces prey sources uphill, suggesting that bats would forage in cove areas in the early evening then move up the mountain as temperature continues to fall in low elevations. Conversely, bats may also avoid steep terrain due to the increased energy demands required to achieve lift (Adams et al., 2012; MacAyeal et al., 2011).

Our data suggest that single-event fires on the landscape have little to no impact on bat occupancy across species through time. However, with the exception of scenic overlooks, our sites were not purposefully managed with fire. Repeated prescribed fire, such as that used restore oak-dominated stands in the central and southern Appalachians, was not addressed in this study (Johnson et al., 2011; O'Keefe, 2009). However, our finding of lack of support for single-event fire after long-term suppression impacts on bats suggests that re-introduction of fire to achieve



land management goals, is unlikely to negatively affect bat foraging habitat. However, there is still a need for research on the effects of repeatedly burned landscapes on bats, because application of fire recommends multiple burns. Hutchinson et al. (2005) found that it required multiple fires over the course of eight years to achieve prolonged reductions in midstory tree basal area and basal sprouting. Current research suggests that bats display species-specific responses to fire that are linked to amount of remaining vegetative clutter (Cox et al., 2016; Owen et al., 2004).

Relative bat activity levels of WNS-affected species, while not a focal point of this study, have been documented as currently very low in the Central Appalachians (Austin et al., 2017b) and other WNS-affected areas (Brooks, 2011; Dzal et al., 2011; Ford et al., 2011; Jachowski et al., 2014). We also documented low activity levels of WNS-affected species. Population declines are known to have occurred as a result of WNS (CITATION). Though the link between abundance and occupancy is unclear, low occupancy rates in our study area likely also reflect WNS declines.

Maximizing detection rates is essential in the face of WNS-related bat declines and the increasing level of effort required to detect a present species (Coleman et al., 2014b). For example, we found that detection probability decreased with increasing wind speed for the eastern red bat, which is likely a function of microphone interference. Eastern small-footed detection probability increased with temperature, likely as a result of increased insect prey activity (Lemoine et al., 2014). We found detection of northern long-eared bats, little brown bats, and tricolored bats to be positively related to tree density, whereas Ford et al. (2005) and Owen et al. (2004) noted these species in cluttered to moderately cluttered environments more than in open areas or clearcuts within the central Appalachians. Likewise, O’Keefe et al. (2014) found

an inverse relationship between detection and basal area in the southern Appalachians. It is unclear why our results differed from these other studies, but may be because our statistical approach directly accounted for detection. Detection of Indiana bats also increased with increasing canopy cover, which may be a function of the high canopy, characteristic of the older-aged forests found in our study area, pushing bats down towards detectors into the more open midstory and subsequent foraging space below. Ford et al. (2005) found a similar relationship between Indiana bat occupancy and canopy cover.

Our study highlights the need for continued refinement in the use of automated software identification programs relative to the effect of false-positive and false-negative determinations for sampled species. Though both programs we used have been found to have moderate to high classification accuracy rates for bat communities in the region (Ford, 2014), our finding of high likelihood of false positive identification of Indiana bats when little brown bats were present suggests that software users should be particularly cautious interpreting survey results. Due to sample size limitations, we could not consider all of the false-positive covariates of interest such as total bat community activity and total Myotis activity (Broders et al., 2004; Clement et al., 2014); further work with false-positive detections is needed both for analysis and interpretation.

Much of our current understanding on the impacts of fire in the central Appalachians and elsewhere in the East has focused most on impacts to day-roosting habitat (Boyles and Aubrey, 2006; Ford et al., 2016a; Johnson et al., 2009, 2010b, 2012; Silvis et al., 2016a). Response of bats to fire in terms of roost use and roost creation is well known and largely neutral to positive, depending on species (Ford et al., 2006, 2016a; Harper et al., 2016; Johnson et al., 2009, 2010b). Our research helps clarify the impacts of fire on bat foraging habitat at long time scales. We found no evidence of fire impacts, long or short term, on the foraging behavior and activity

northern long-eared, tricolored, eastern small-footed, and eastern red bats, and evidence of very limited effects of fire on this with hoary, Indiana, big brown, and little brown bats. Nonetheless, owing to the diversity of the bat fauna and complexities of the landscape response to either wildfire or prescribed fire, additional research examining fire on bat foraging and roosting habitat is warranted.

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### **Chapter 3: Bat Activity Following Restoration Prescribed Burning in the Central Appalachian Upland and Riparian Habitats**

#### *Abstract*

After years of fire suppression beginning in the early to mid-20<sup>th</sup> century in eastern North America and elsewhere, land managers now are prioritizing prescribed fire as a management tool to maintain fire-adapted vegetation communities. However, it is unknown how bats will respond to prescribed fire in riparian and upland habitats. To address these concerns, we used paired sampling to monitor bat activity in burned, unburned, riparian, and non-riparian areas. Burn and riparian variables had empirical support ( $\Delta AICc < 4$ ) to explain activity of all bat species. Nonetheless, parameter estimates for these conditions were small and confidence intervals overlapped zero for all species, indicating that the effect was marginal. Our results suggest bats respond to fire that differently between upland and riparian habitats, but that large landscape level prescribed fire has a slightly positive to neutral impact on all bats species identified in at our study site post-fire suppression.

#### *Introduction*

Riparian zones are particularly important for bats because they serve as travel corridors (Grindal et al., 1999), primary foraging areas (Ford et al., 2005; Fukui et al., 2006; Monadjem and Reside, 2008), as well as water sources, and for some species, day-roost site (Swystun et al., 2007). In most environments, bat activity generally is higher in riparian habitat compared to upland habitat (Grindal et al., 1999; Menzel et al., 2005; Monadjem and Reside, 2008; Owen et al., 2004; Rogers et al., 2006), which has been attributed to the abundance of insects in riparian

areas that provide an important prey resource for bats (Almenar et al., 2013; Carter et al., 2003; Fukui et al., 2006). Fukui et al. (2006) found that bat activity is correlated to insect abundance in riparian habitats, and in coastal swamp forest and saltmarsh habitats Gonsalves et al. (2013) showed that bats shifted foraging range to account for differences in insect abundance. Almenar et al. (2013) suggests that bats hierarchically select riparian habitat patches with physical structures that facilitate prey accessibility and detectability. Physical characteristics (i.e., water turbulence, bank steepness; (Hagen and Sabo, 2014; Lundy and Montgomery, 2010; Rydell et al., 1999), stream order (Ford et al., 2005; Johnson et al., 2010b; O’Keefe et al., 2013; Seidman and Zabel, 2001), and vegetative cover (Akasaka et al., 2010; Monadjem and Reside, 2008; Ober and Hayes, 2008) may determine how bats use riparian areas to access insect prey.

After years of fire suppression beginning in the early to mid-20<sup>th</sup> century in eastern North America and elsewhere, land managers now are prioritizing prescribed fire as a management tool to maintain fire-adapted vegetation communities or to impede the transitioning of fire-dependent communities to other types, i.e., mesic communities with little or no oak (*Quercus* spp.; Block et al., 2016; Hessburg et al., 2016; Hessler et al., 2011; Iverson et al., 2017; Nowacki and Abrams, 2008; Strahan et al., 2015; USDA Forest Service, 2006). However, unlike other taxa, fire effects on bats in many forest ecosystems have been relatively poorly studied and many questions exist (Carter et al., 2000). Moreover, with tremendous stressors impacting bats presently in eastern North America from White-nose Syndrome mortality (Francl et al., 2012; Frick et al., 2015; Ingersoll et al., 2016) and population declines as well as wind energy development (Arnett and Baerwald, 2013; Erickson et al., 2016), the need to understand fire impacts on bat assemblages, as well as habitat use and distribution has become even more urgent (Francl et al., 2012; Frick et al., 2015; Ingersoll et al., 2016).

Depending on forest type and landscape setting, bats are likely to respond to fire differently between riparian and upland habitat. For example, a single event fire in the southern Appalachian mountains, after 70 years of suppression, resulted in 37% tree mortality in upland habitat but no mortality in riparian habitat (Elliott et al., 1999), indicating perhaps little change to potential day-roost availability or change in foraging conditions therein. However, we would expect that repeated prescribed burning results in reduced regrowth when compared to single-event prescribed fire or wildfire (Hutchinson et al., 2005). There has been very limited research on the effect of repeated, short-interval fire restoration landscapes on bat communities in the temperate deciduous forests of the Appalachians, particularly in regard to foraging habitat. Johnson et al. (2009, 2010b) found that two *Myotis* species, MYSE and MYSO, readily utilized fire-killed trees as roosts in habitat with reinstated prescribed fire ( $\leq 3$  yrs of annual treatment). In the Ozark mountain region of Missouri, Boyles and Aubrey (2006) found a total of 63 evening bat (*Nycticeius humeralis*) roosts, all of which were located in habitat subjected to several years of biennial prescribed fire. Bat activity in the Chicago metropolitan area was positively associated with repeated prescribed fire (Smith and Gehrt, 2010), while bat activity in long-leaf pine and wiregrass ecosystem was lower in sites with longer fire-return intervals (Armitage and Ober, 2012). Fire changes to roost availability could result in increased bat activity as bats commute between roosting and foraging areas.

Although fire has the potential to negatively impact bats through direct mortality, habitat loss, and disruption of group dynamics (Boyles and Aubrey, 2006; Carter et al., 2000; Ford et al., 2016a), most research has shown that fire may actually benefit bats through roost creation and clutter reduction (Ford et al., 2006, 2016a; Perry, 2012) or have a neutral effect on bats (Buchalski et al., 2013; Johnson et al., 2010b), depending on species. Generally, overall bat



activity in burned upland habitat has been documented as higher than in unburned upland habitat (Armitage and Ober, 2012; Loeb and Waldrop, 2008; Silvis et al., 2016a; Smith and Gehrt, 2010), with species-specific responses linked to variation in reduction of vegetative clutter (Cox et al., 2016; Owen et al., 2004). Morphology and call structure (Aldridge and Rautenbach, 1987; Norberg and Rayner, 1985) as well as competition for resources (Razgour et al., 2011) also influence bat habitat selection and partitioning among bat species relative to how fire modifies the post-burn landscape.

Prescribed fire often provide benefits to insect taxa that serve as bat prey species, through proliferation of nectar-producing plants (Rudolph and Ely, 2000) and herbaceous growth that provides substrate on which to lay eggs (Evans et al., 2013). Arthropod responses to fire are variable depending on species, life history stage, location, and burn season (Warren et al., 1987). Abundance of ground and litter dwelling arthropods is greatly reduced post-fire, however diversity, richness, and evenness were less affected by fire (Rieske-Kinney, 2006). Siemann et al. (1997) found that species that were less abundant the growing season immediately post-burn, were typically more abundance in areas subjected to more frequent fires in the past 30 years. Short generation time and the ability of aerial insects to quickly recolonize, may ameliorate immediate reductions in insect prey sources for bats.

To date, the majority of research on fire effects on bats has been focused either across whole landscapes or more narrowly upland habitats, despite clear importance of riparian habitats to bats. This is particularly true for federally protected bat species such as the Indiana bat (*Myotis sodalis*; MYSO) and northern long-eared bat (*Myotis septentrionalis*; MYSE; Ford et al. 2005; Carter 2006; Johnson et al. 2010) in the Central Appalachians where fire use on public land has increased greatly over the past two decades. Nonetheless, presence of these two species often

causes consequential regulatory restrictions on prescribed fire use in terms of seasonality, frequency, and extent (Carter et al., 2000; Ford et al., 2016a). To investigate this where both species are known to be present in the central Appalachians of western Virginia, we used a paired sampling design to observe bat activity in repeatedly burned and unburned, riparian and non-riparian areas. Based on previous research on bat-specific habitat correlates in the central Appalachians (Ford et al., 2005), we predicted that responses to repeated prescribed fire in both riparian and non-riparian habitats would be species-specific, with larger-bodied bats like the hoary bat (*Lasiurus cinereus*; LACI), the big brown bat (*Eptesicus fuscus*; EPFU), and the silver-haired bat (*Lasionycteris noctivagans*; LANO) displaying greater activity in burned and riparian areas than unburned and non-riparian areas due to reduced vegetative clutter, and the relatively clutter-adapted *Myotis* species and the tricolored bat (*Perimyotis subflavus*; PESU) to display a neutral response to fire. We predicted that the eastern red bat (*Lasiurus borealis*; LABO) also would display a neutral responses to fire reduced clutter and riparian areas, as seen in previous research (Ford et al., 2005; Menzel et al., 2005).

## *Methods*

### *Study Area*

We conducted our study on the George Washington National Forest (GWNF) in the Warm Springs Ranger District in Bath County, Virginia, USA (Figure 3-4). This portion of the GWNF lies within the Ridge and Valley subprovince of the Appalachian Mountains (Fenneman, 1938). The dominant surface geology is resistant sandstone ridges and limestone valleys and there are numerous karst caves that serve as hibernacula for bats (White, 2015). Mountains form of long, linear ridges (Simon et al., 2005) with elevations that range from 450 to nearly 1,300 m.

An ~8000 ha portion of the GWNF, located adjacent to the Warm Springs Mountain Preserve, is cooperatively managed by USDA Forest Service, The Nature Conservancy (TNC), Virginia Department of Game and Inland Fisheries and Virginia Department of Conservation and Recreation in terms of landscape-level restoration prescribed fire to restore or maintain dry-mesic oak and montane pine associations (Braun, 1950). In burned areas, bear oak (*Quercus ilicifolia*), table mountain pine (*Pinus pungens*), and pitch pine (*Pinus rigida*) are present, with chestnut oak (*Quercus prinus*) and white oak (*Quercus alba*) as the dominant species. Blueberries occur as understory vegetation in fire dependent plant communities. Mesic, shade-tolerant white pine (*Pinus strobus*) and eastern hemlock (*Tsuga canadensis*) occur at low elevations and in riparian corridors. Fire suppression policies from the 1920s to the beginning of the 21<sup>st</sup> Century has impacted forest composition and structure by increasing abundance of more mesic, fire-intolerant species such as red maple (*Acer rubrum*), American beech (*Fagus grandifolia*), blackgum (*Nyssa sylvatica*), and tulip poplar (*Liriodendron tulipifera*). Locally, prescribed fires typically are lit via aerial ignition in March and April of each year to meet management goals that include preservation of biodiversity, control of invasive plant species, and restoration of historic fire regimes (3-9 years) in fire-dependent pine and oak forests (M. Smith, TNC, pers. comm.; (USDA Forest Service, 2015).

#### *Data Collection*

Following the protocol of Ford et al. (2005) we collected call data, site location, and canopy closure at each survey site. To assess bat activity, we recorded bat activity from 17 May through 4 August 2016 using acoustic detectors (Songmeter ZC; Wildlife Acoustics, Maynard, Massachusetts, USA<sup>4</sup>). We programmed acoustic detectors to record data from 2000 to 0700 hours

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<sup>4</sup> The use of any trade, product or firm names does not imply endorsement by the US government.

at 10 areas where a stream and corresponding riparian conditions extended from an unburned forest to a burned forest. We placed four detectors in each area, one in burned/riparian, burned/non-riparian, unburned/riparian, and unburned/non-riparian forest habitat, for a total for 40 detector locations (Figure 3-1). Our study sites consisted of nine first order intermittent streams and one second order stream. We blocked by each group of habitat configurations (i.e., a site with 4 detectors one in each burned/riparian, burned/non-riparian, unburned/riparian, and unburned/non-riparian forest habitat) to minimize landscape effects and enable us to attribute bat activity differences to riparian and burn variables of interest (Figure 3-2). All detectors were spaced a minimum distance of 80 meters to ensure that detectors did not record the same bat simultaneously. We selected riparian areas using 2014 TIGER/Line shapefiles for Bath County, Virginia available online through the U.S. Census Bureau, Department of Commerce (<https://catalog.data.gov/dataset/tiger-line-shapefile-2014-county-bath-county-va-linear-hydrography-county-based-shapefile>) that were USDA Forest Service owned, and burn history from prescribed burn layers provided by the Forest Service. We measured percent canopy cover at each site using a densiometer ([http://www.forestry-suppliers.com/Documents/1450\\_msds.pdf](http://www.forestry-suppliers.com/Documents/1450_msds.pdf)).

### *Data Analysis*

*Bat Call Identification.* We identified calls using Kaleidoscope version 4.1.0, classifier version 3.1.0 at the sensitive setting (Wildlife Acoustics, Maynard, Massachusetts, United States). We used Kaleidoscopes default signal parameters (8-120 KHz frequency range, 500 maximum inter-syllable gap, 2 minimum number of pulses, enhance with advanced signal processing) and specified nine individual species that we expected to be present at our study site: big brown bats, hoary bats, eastern red bats, silver-haired bats, northern long-eared bats, Indiana bats, little brown bats (*M. lucifugus*; MYLU), eastern small-footed bats (*M. leibii*; MYLE), and

tricolored bats. When visually examining calls, we found a systemic error whereby large quantities of insect noise were consistently being classified as either hoary bat or red bat calls. To account for this issue, we visually examined all calls identified to species by Kaleidoscope using AnalookW v. 3.9f (Titley Electronics, Ballina, NWS, Australia) and removed all erroneously-identified insect noise. After removing noise, we re-ran calls through Kaleidoscope to obtain corrected nightly counts by species.

We documented an unusually high number of LANO calls. In Virginia, this species typically is caught only in May as it migrates through the state (Cryan, 2003), though anecdotal reports of summer captures have occurred (M. St. Germain, Virginia Tech Conservation Management Institute, pers. comm.). Additionally, there is high uncertainty in automated program identification of LANO (Ford, 2014), thus we grouped EPFU and LANO calls. We present results for all *Myotis* species combined to account for program identification uncertainty and all species combined to examine fire and riparian effects on overall bat activity. For all species and species groups, we included random effects to account for blocking and repeated measurements at individual sites (multiple nights). We also included a random effect for burn year (YSB – Years Since Burn). We fit models with using package glmmADMB (Fournier et al., 2012; Skaug et al., 2016) in program R version 3.2.3 (R. Development Core Team, 2014) . We compared models representing competing hypotheses using an information theoretic approach by ranking models using Akaike's Information Criterion corrected for small sample size (AICc; (Burnham and Anderson, 2002)). We identified a confidence set of models within  $\Delta AICc < 4$  as competing models. To account for uncertainty in the model selection process we used package MuMIn (Barton, 2016) in program R to obtain full model averaged estimates, unconditional standard errors, and 95% confidence intervals to assess individual variable effects on bat activity

levels for all species and species groups of interest (Grueber et al., 2011; Symonds and Moussalli, 2011).

*Vegetation Configuration.* We compared canopy cover among our four habitat configurations using multiple linear mixed models; we included a random effect to account for area blocking. We determined effect sizes by comparing centered and scaled fitted estimates for canopy cover. We fit models in program R using package lme4 (Bates et al., 2015) and obtained R-squared values using package MuMIn (Barton, 2016). We selected canopy cover as a measure of fire effects on vegetation because changes occur within a relatively short period of time (i.e., tree senescence or mortality with subsequent leaf fall). Comparing variations in canopy cover to the different habitat configurations enables us to relate differences in bat activity between riparian and burn habitats to vegetative characteristics.

## *Results*

At 40 acoustic detection points in burn/riparian, burn/non-riparian, unburned/riparian, and unburned/non-riparian forest stands, we accumulated 738, 660, 724, and 764 recording nights, respectively. Differences in sampling duration between habitat configurations were due to periodic detector failures. After visual noise removal, Kaleidoscope identified 11,689 total bat call files and assigned them to nine unique species: EPFU (4,989), LABO (1,831), LACI (355), LANO (2,289), MYLE (134), MYLU (682), MYSE (348), MYSO (341), and PESU (720). We had to exclude YSB in models for LACI, LABO, EPFU/LANO, and total bat activity due to model convergence errors.

All models for all species and species groups were highly competitive and consequently had empirical support ( $\Delta AICc < 4$ ), except the riparian model for LACI (Table 3-1). Burn and

riparian variables and their interaction had slight positive effects for all species and groups. While burn and riparian variables had a slight positive effect on EPFU/LANO, LACI, and total bat activity, the interaction between burn and riparian variables had a slight negative effect. Nonetheless, coefficients were small and confidence intervals overlapped zero indicating that the effect was marginal (Table 3-2; Table 3-3). The riparian condition variable had a marginally negative effect on LACI though confidence intervals overlapped zero. Overall, burn and riparian variables had a slight positive to neutral effect on the activity of all species combined albeit with small coefficients and confidence intervals overlapping zero.

For canopy cover, over 20% of the variation therein was explained by habitat configuration ( $R^2=0.21$ ). Canopy cover was lower in burned areas than unburned areas (Figure 3-3). Within the burned areas, non-riparian areas had less canopy cover than riparian areas. Unexpectedly, we found that within the unburned areas, riparian areas generally had less canopy cover than non-riparian areas.

## *Discussion*

We found little evidence of fire effects for EPFU/LANO and LACI. For both species/groups, the relationship was positive, but only marginally. In absolute terms activity was higher in recently burned stands than in adjacent or nearby unburned forests. This result is somewhat consistent with our expectation that larger-bodied and less maneuverable bats would benefit from clutter reduction resulting from prescribed fire and thinning treatments (Loeb and Waldrop, 2008; Silvis et al., 2016a). Indeed, we documented less canopy cover clutter in recently burned habitats (2008-2014), likely due to post-fire canopy die-back as well reduction in stem density from tree mortality and bole loss. Previous research in the South Carolina Piedmont

showed significantly higher levels of bat activity for both EPFU and LABO in burned, thinned, and burned/thinned stands compared to control stands (Loeb and Waldrop, 2008). Additionally, research in the Ohio hills showed higher levels of EPFU activity in thinned and thinned/burned treatments compared to control treatments (Silvis et al., 2016a), suggesting that this phenomenon cuts across physiographic provinces.

In contrast, riparian areas had only a marginally positive effect on EPFU/LANO and a marginally negative to neutral effect on LACI. Previous research has shown that LACI utilize long-range echolocation and a rapid, straight pursuit technique (Barclay, 1985). Our study consisted of nine first order streams and one second order stream, thus it is possible that riparian corridors were too small to support LACI flight and/or foraging strategies.

We propose two possible explanations for our observed negative interaction between riparian and prescribed fire conditions for LACI and EPFU/LANO relative to prey availability and habitat quality. First, while previous research has found fire to have a positive impact on the dominant prey species of LACI and EPFU/LANO in upland habitats (Armitage and Ober, 2012; Campbell et al., 2008; Evans et al., 2013; Rudolph and Ely, 2000), reductions in fire severity of riparian habitats as compared to upland habitats (Halofsky and Hibbs, 2008; Pettit and Naiman, 2007) may not provide the same benefits to the insect communities that serve as a prey base for LACI and EPFU/LANO. Conversely, in riparian areas, bats may shift focus to more abundant aquatic-associated insect species, which may be negatively influenced by fire depending on severity (Malison and Baxter, 2010), ash deposition, or reductions in dissolved oxygen (Earl and Blinn, 2003). However, in Appalachian systems overall aquatic environment seems little changed post-fire (Vose et al., 2005). Second, fire may impact the vegetative community of riparian areas differently than in upland communities. There is evidence that the mesic soil of



riparian habitats promotes regrowth of vegetation (Brown and Peet, 2003; Dwire and Kauffman, 2003) which could impede flight and foraging of larger bodied bats.

Consistent with our predictions based on body size and habitat selection, we found little evidence of fire, riparian, or interaction effects on activity levels of *Myotis* species both jointly and individually, PESU, and LABO. Estimands of burn condition for all species, except MYSO, were smaller than those of the larger bodied species EPFU/LANO and LACI. *Myotis* species and PESU are generally considered clutter-adapted based on morphology and call structure, with MYSE and MYLU utilizing vegetation for gleaning insects (Ratcliffe and Dawson, 2003). The highest ranking model for MYSE was the null, possibly because this species is a habitat generalist within forested conditions (Silvis et al., 2016b). Previous research has shown that LABO and PESU have similar activity in both upland and riparian habitat as well as cluttered and open habitat (Ford et al., 2005; Menzel et al., 2005). In the eastern United States, *Myotis* activity was similar between burned and unburned upland habitat (Cox et al., 2016; Silvis et al., 2016a), whereas research in the western United States found overall activity to be higher in burned habitat than unburned upland habitat with species-specific responses to fire severity among myotids (Buchalski et al., 2013). This is consistent with our finding of negligible impacts of fire (in both upland and riparian areas) on these species.

Regardless, overall bat activity at our sites was low, irrespective of prescribed burning and riparian status, for all *Myotis* species and PESU. This primarily can be attributed to White-nose syndrome related mortality (Francl et al., 2012; Reynolds et al., 2016), but also to mortality at wind energy facilities (Erickson et al., 2016), and the small size and intermittent nature of streams at our study site which may not have provided enough contrast to surrounding upland conditions. Although, O’Keefe et al. (2013) documented minimal use of riparian areas associated

with small streams in the Appalachians for MYSE and MYSO, others have found these areas to be important (Ford et al., 2005, 2016b). More generally, however, there is evidence that bat activity is positively related to stream order (Lloyd et al., 2006). Incorporation of higher order streams may have resulted in higher bat activity, however fire is typically excluded in the riparian zones of the Appalachians to be consistent with current best management practices and thus would not have allowed for comparison of fire effects between upland and riparian habitats.

Our results suggest bats respond to fire that differ between upland and riparian habitats, likely due to vegetative clutter and/or insect availability, but that large landscape level prescribed fire has a slightly positive to neutral impact on all bats species identified in at our study site post-fire suppression. This is consistent with day-roost and fire research in the region as well (Ford et al., 2016a; Johnson et al., 2010a). Research in the western US and Ireland has shown that a diversity of riparian habitat is needed to support a diverse bat community (Lundy and Montgomery, 2010; Ober and Hayes, 2008), and because fire intensity and severity is affected by environmental factors within the riparian zone, it is capable of creating a mosaic of habitats (Pettit and Naiman, 2007), likely suitable for the diverse bat community found in the Appalachians.

Prescribed fire is used to meet many land management goals: conservation of fire-dependent, oak-dominant communities, preservation of biodiversity, control of invasive plant species, and restoration of historic fire regimes in fire-dependent pine and oak forests. However, fire faces regulatory restriction due to presence of listed bat species. Research examining the impacts of fire on bat foraging habitat in the central Appalachians is restricted to upland habitats (Armitage and Ober, 2012; Cox et al., 2016; Smith and Gehrt, 2010). Our research helps to elucidate effects of prescribed fire in upland versus riparian habitat on bat activity. Our results

indicate that fire in both riparian and upland habitat appears to have a neutral to positive effect on bat foraging habitat. Thus, bats should not be a strong consideration in modifying plans for use of fire on the Appalachian landscape. Still, additional research on the impacts of prescribed fire on bat roosting habitat of a wider array of species, in riparian and upland areas, would aid land managers in decision making processes regarding prescribed fire regimens.

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## Figures

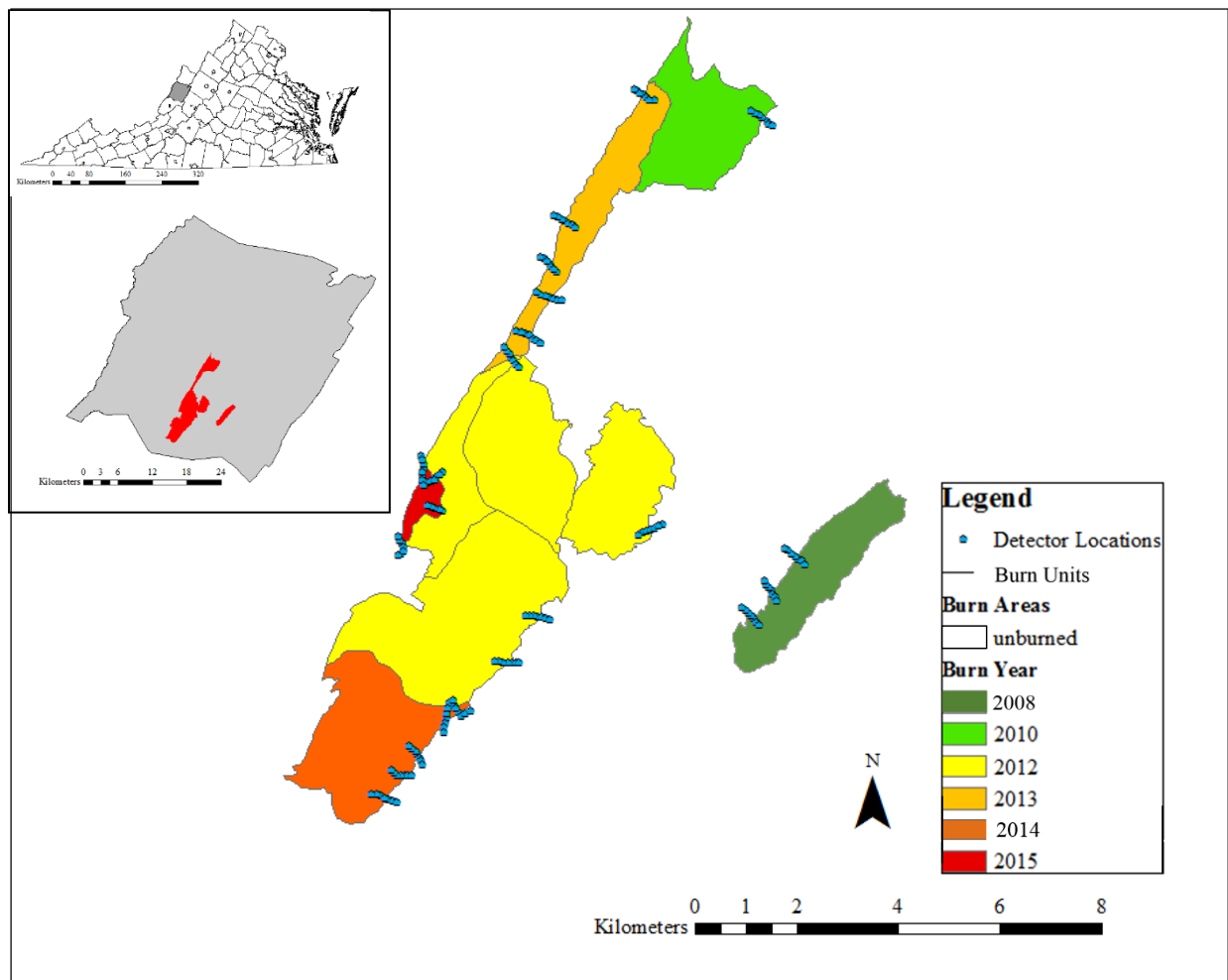


Figure 1-1 Map of bat detector and burn plot locations (color-coded by year last burned) in the Warm Springs Mountain portion of Bath County, Virginia, USA from 24 May to 15 August of 2015. Insets show the location of Bath County within Virginia and the study area within Bath County.

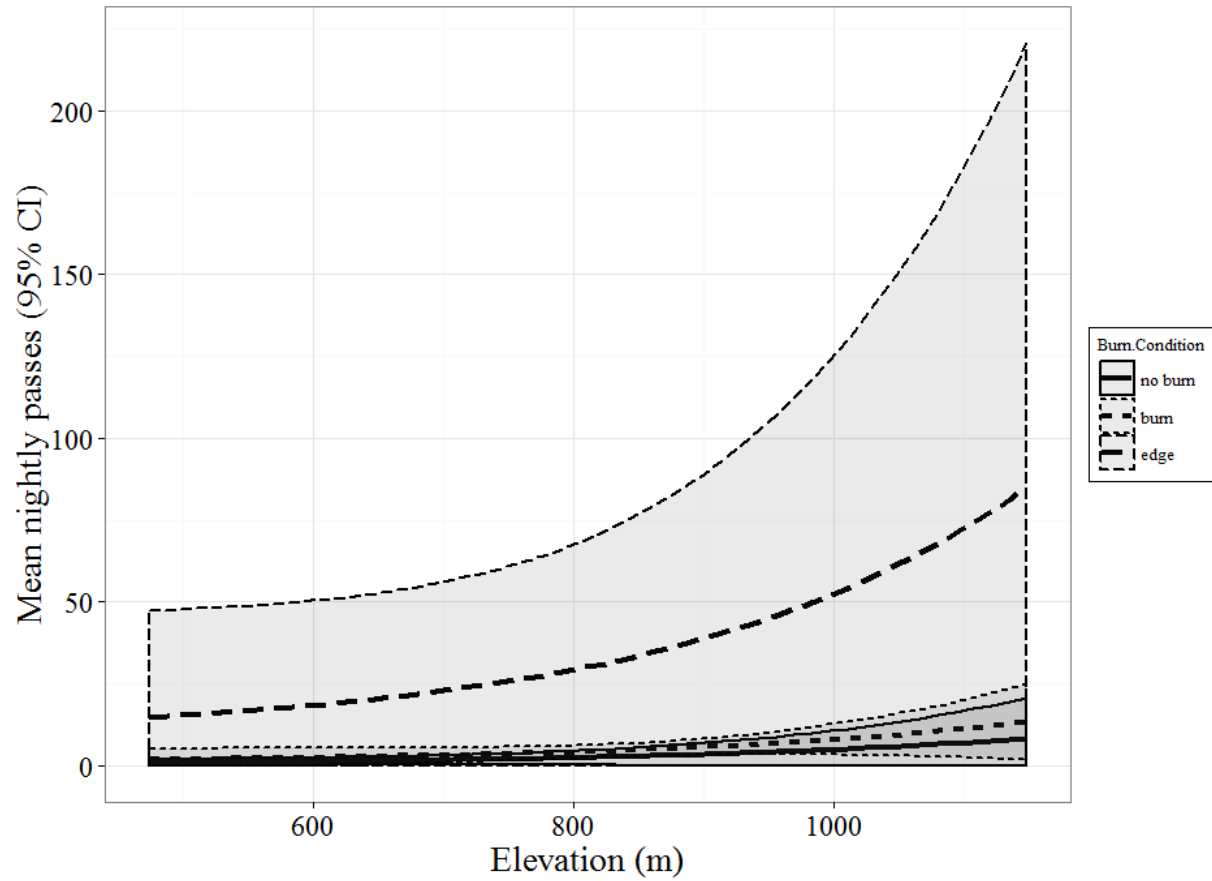


Figure 1-2 Relationship between total mean nightly passes (with 95% CI) and elevation (m) in the Warm Springs Mountain portion of Bath County, Virginia, USA, 24 May to 15 August 2015.

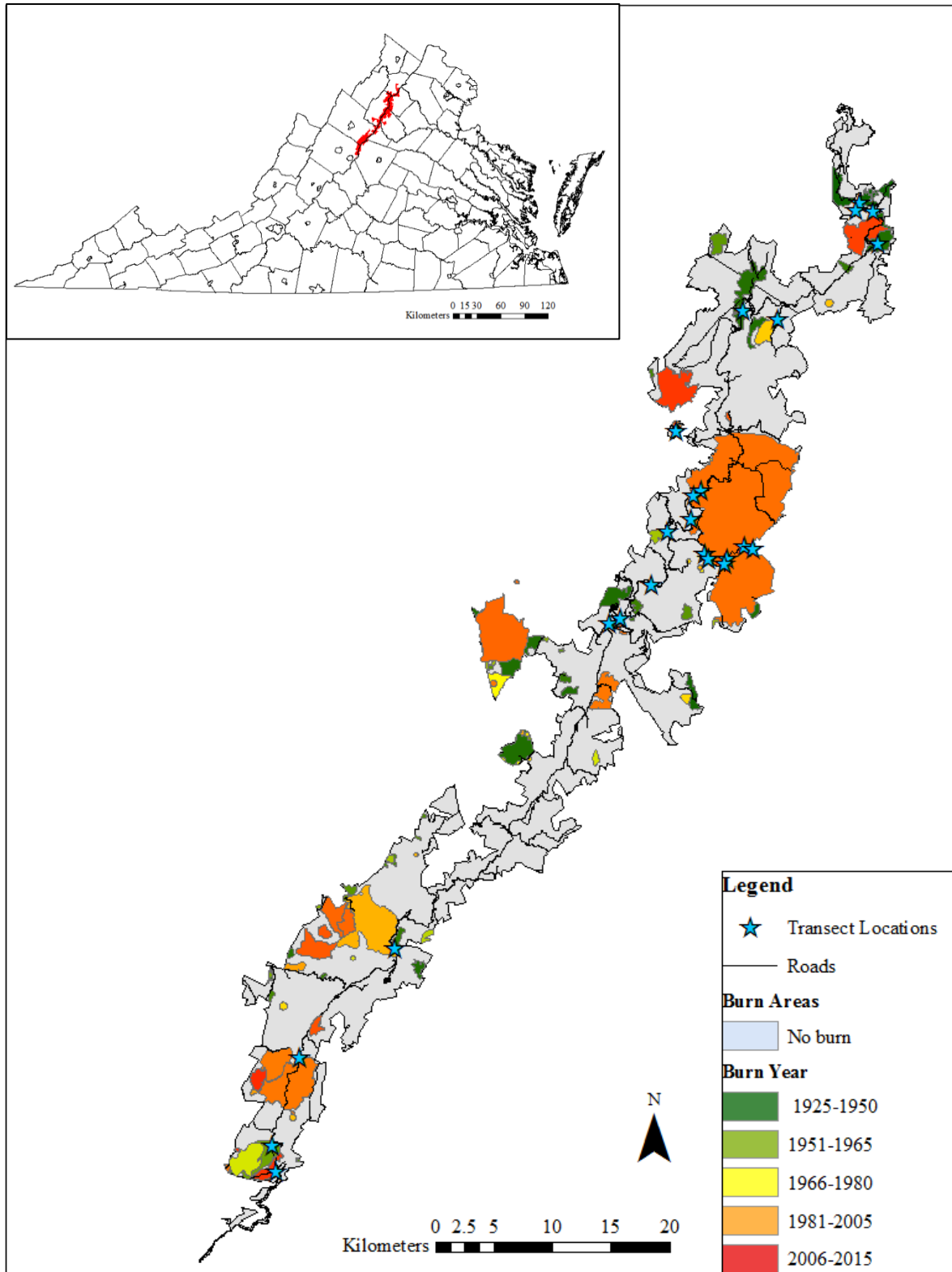


Figure 2-1 Map of bat detector and burn plot locations in Shenandoah National Park, Virginia, USA from 11 June to 15 August of 2015.



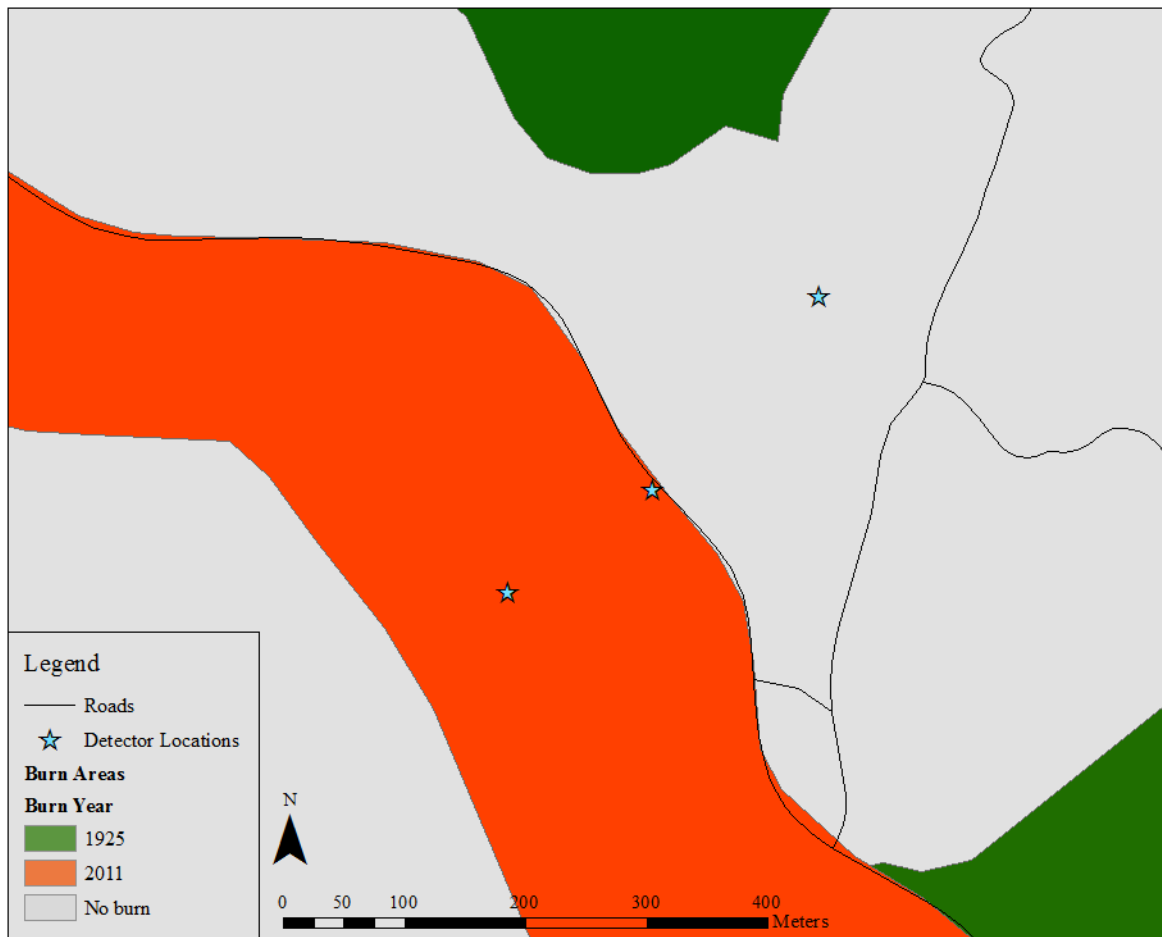


Figure 2-2 Example bat acoustic transect deployed at Shenandoah National Park, VA, USA, in the summer of 2015. Example bat acoustic transect deployed at Shenandoah National Park, VA, USA, 11 June to 15 August 2015.

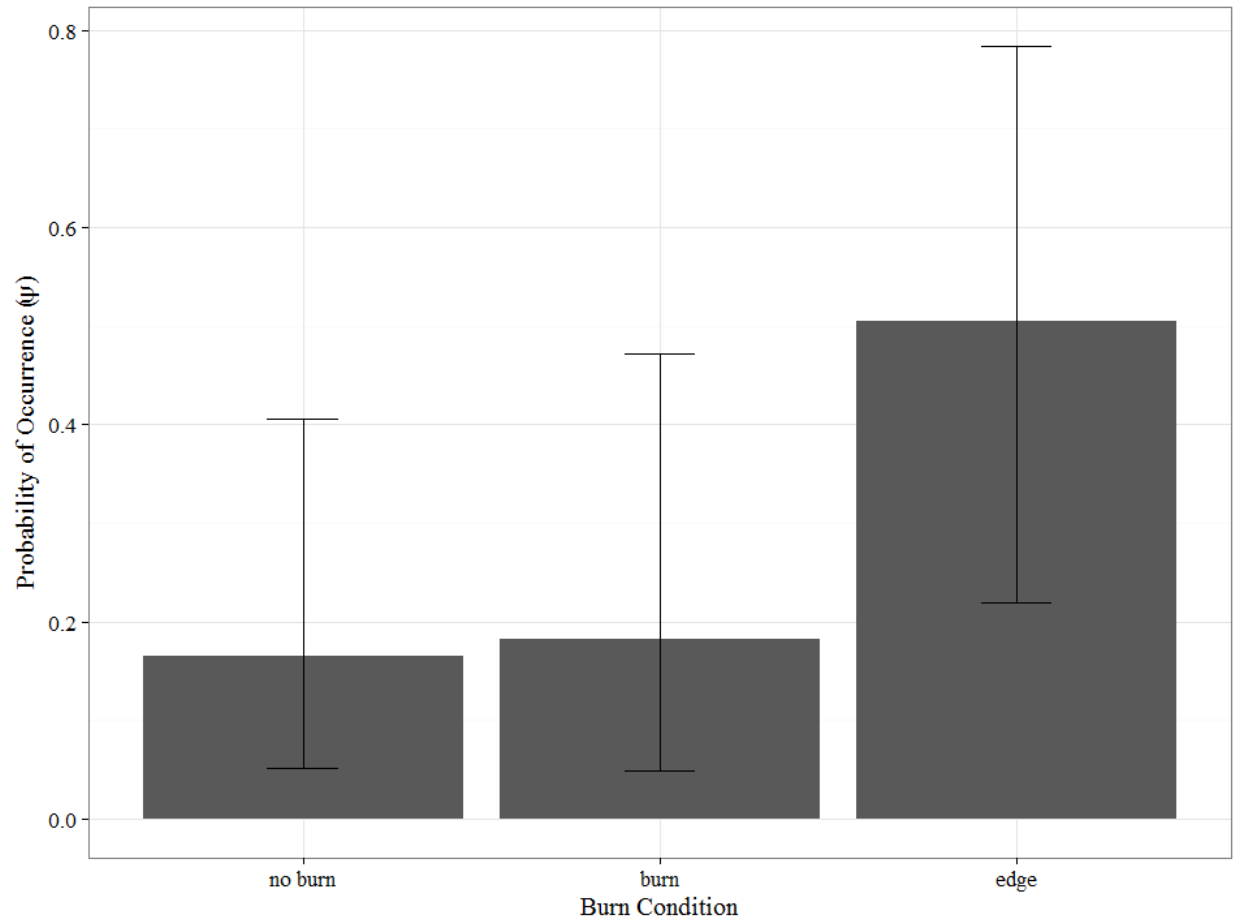


Figure 2-3A Partial effects plot of the relationship between probability of occurrence of big brown bats (with 95% confidence intervals) and burn condition at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model; other covariates were set at mean observed value.

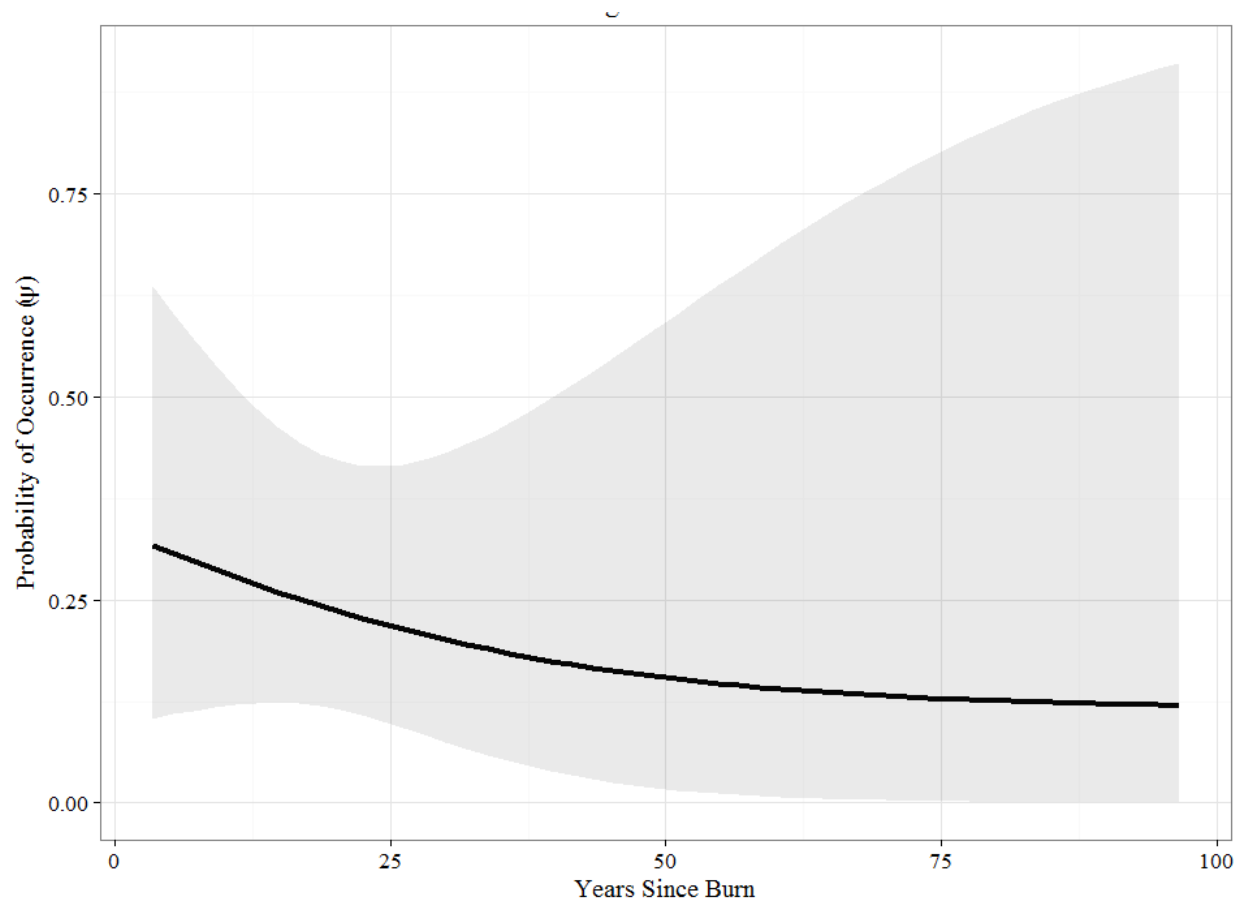


Figure 2-3B Partial effects plot of the relationship between probability of occurrence of big brown bats (with 95% confidence intervals) and years since burn at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model; other covariates were set at mean observed value.

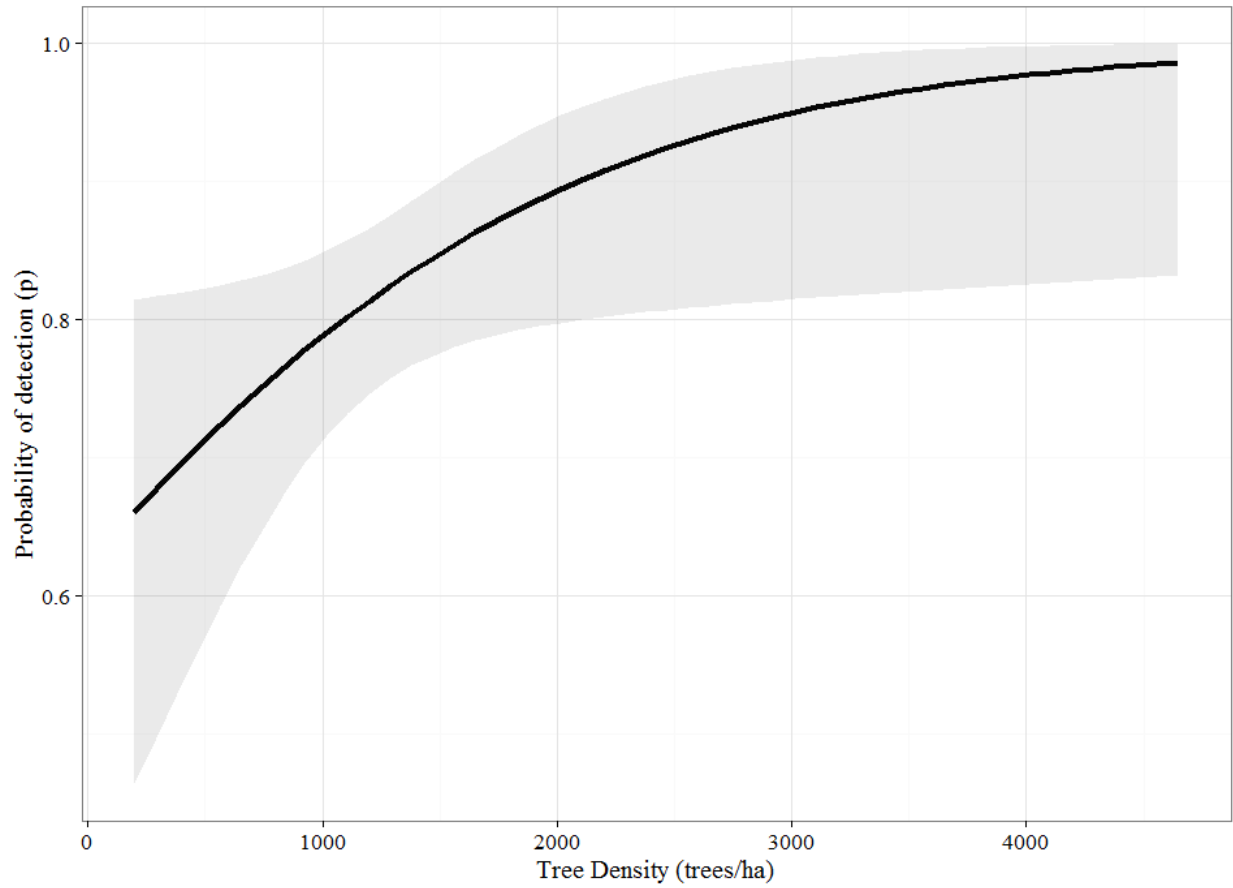


Figure 2-3C Partial effects plot of the relationship between probability of detection of big brown bats (with 95% confidence intervals) and tree density (trees/ha) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

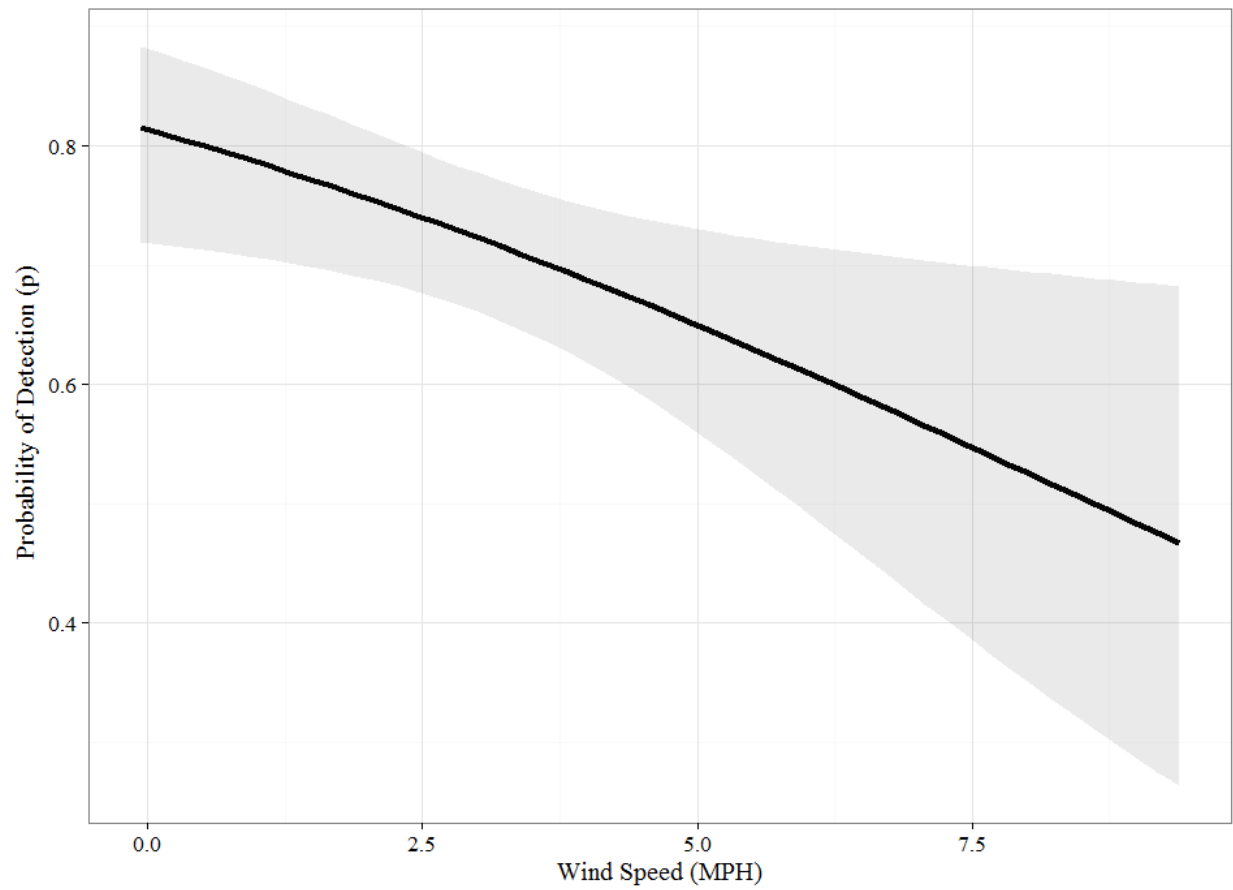


Figure 2-4 Partial effects plot of the relationship between probability of detection of eastern red bats (with 95% confidence intervals) and mean wind speed (MPH) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

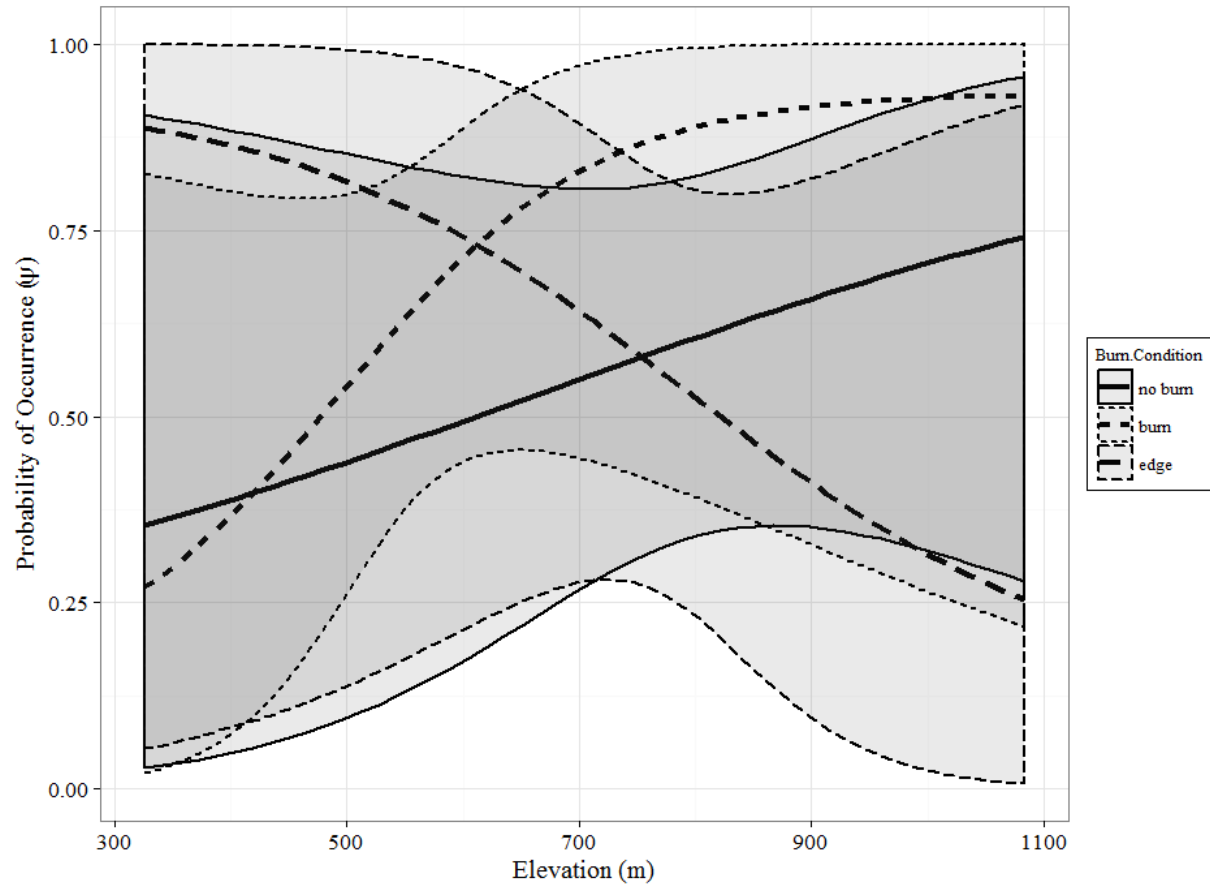


Figure 2-5 Partial effects plot of the relationship between probability of occurrence of hoary bats (with 95% confidence intervals) and an interaction between burn condition and elevation (m) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model; other covariates were set at mean observed value.

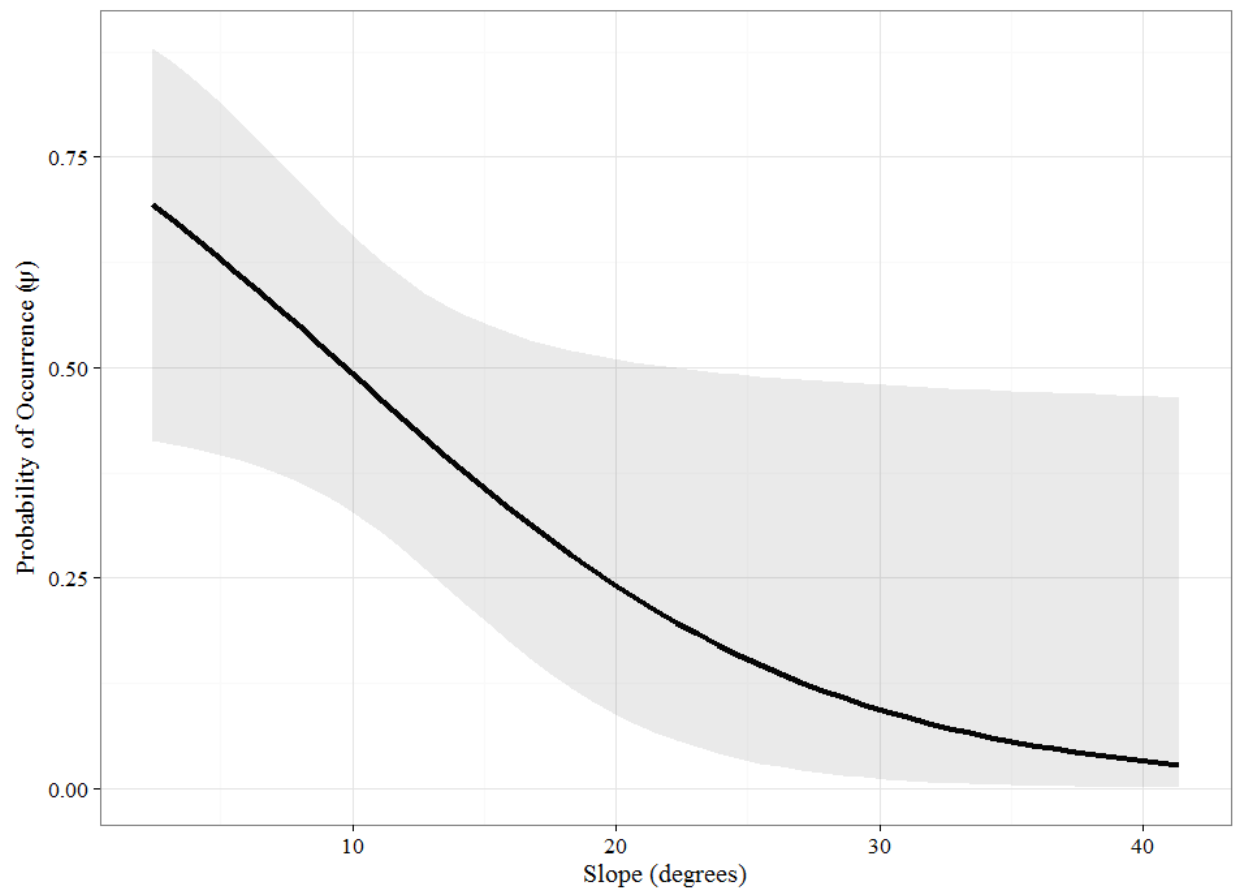


Figure 2-6A Partial effects plot of the relationship between probability of occurrence of eastern small-footed bats (with 95% confidence intervals) and slope (degrees) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

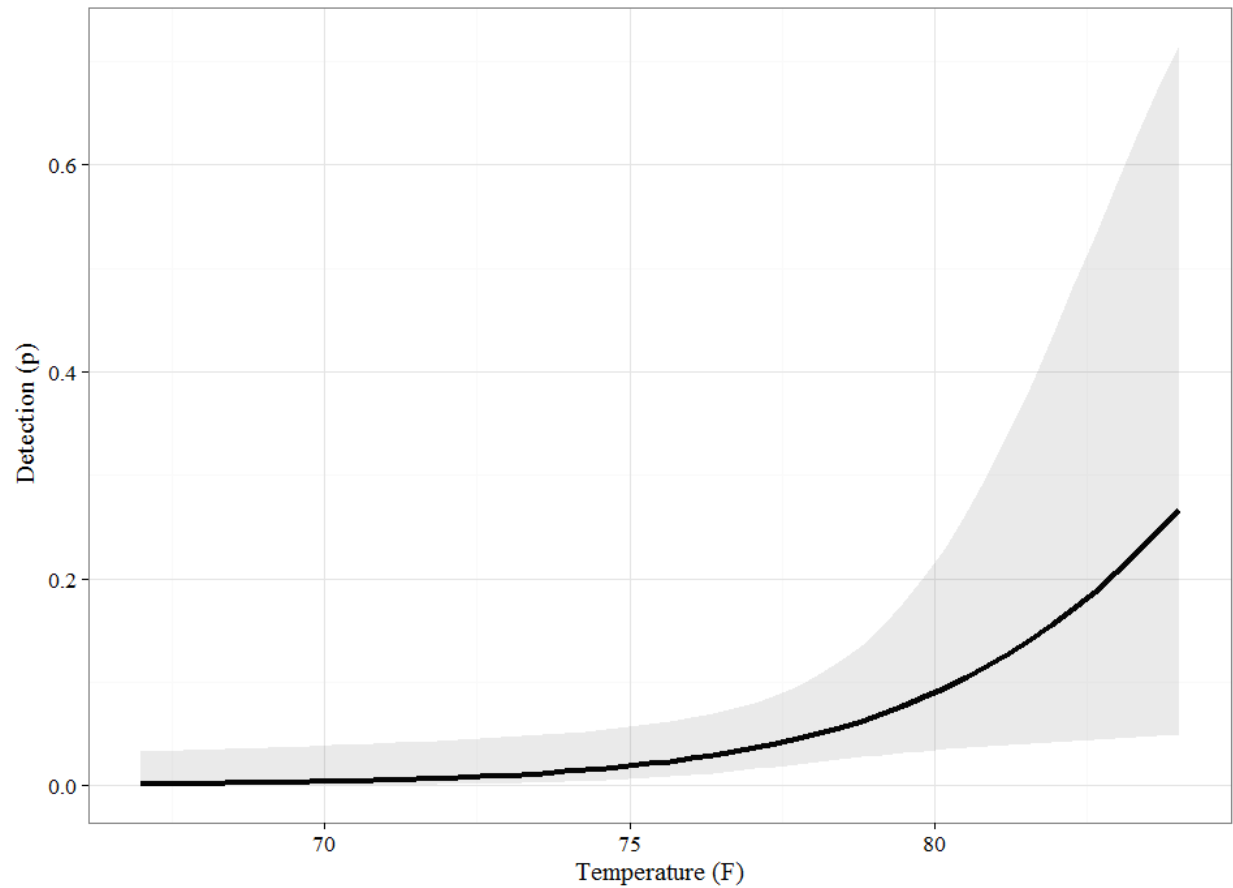


Figure 2-6B Partial effects plot of the relationship between probability of detection of eastern small-footed bats (with 95% confidence intervals) and temperature (F) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.



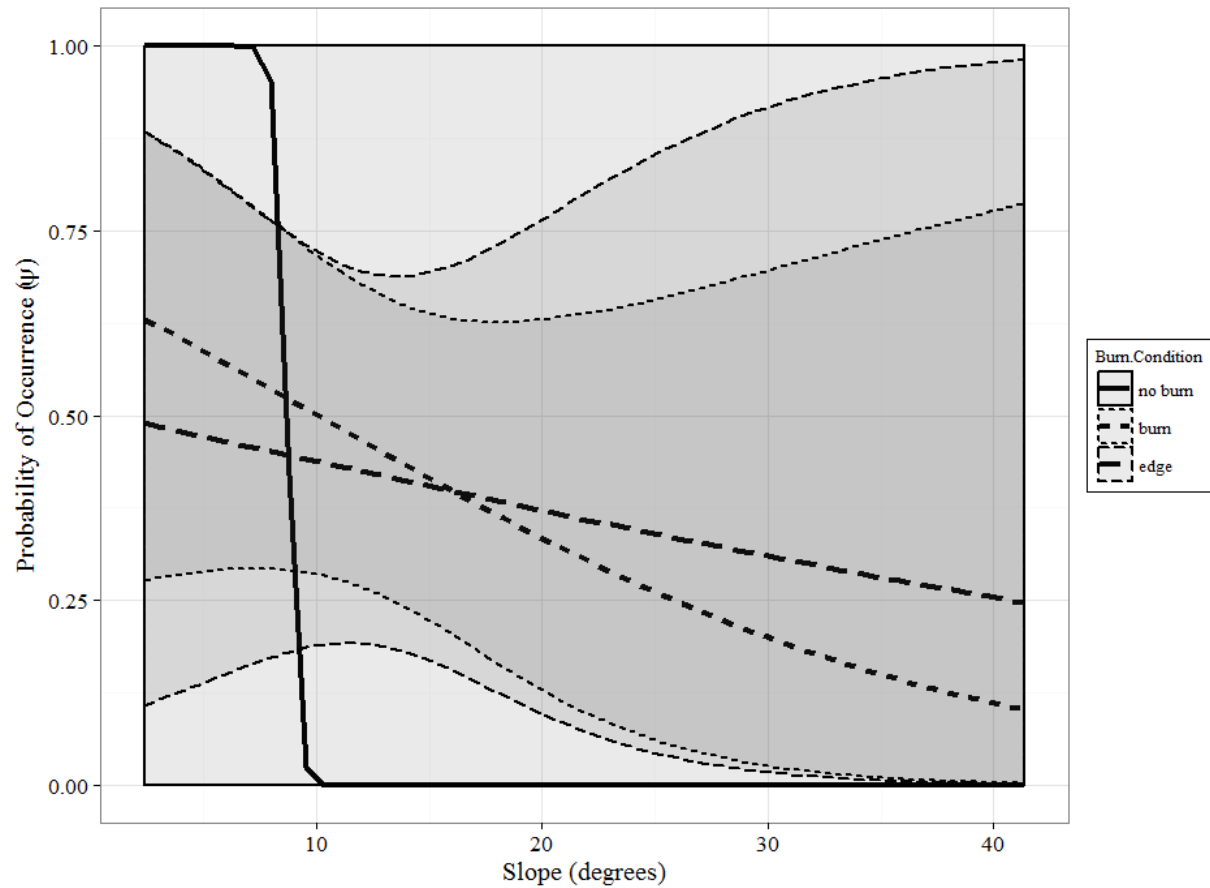


Figure 2-7A Partial effects plot of the relationship between probability of occurrence of little brown bats (with 95% confidence intervals) and an interaction between burn condition and slope (degrees) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

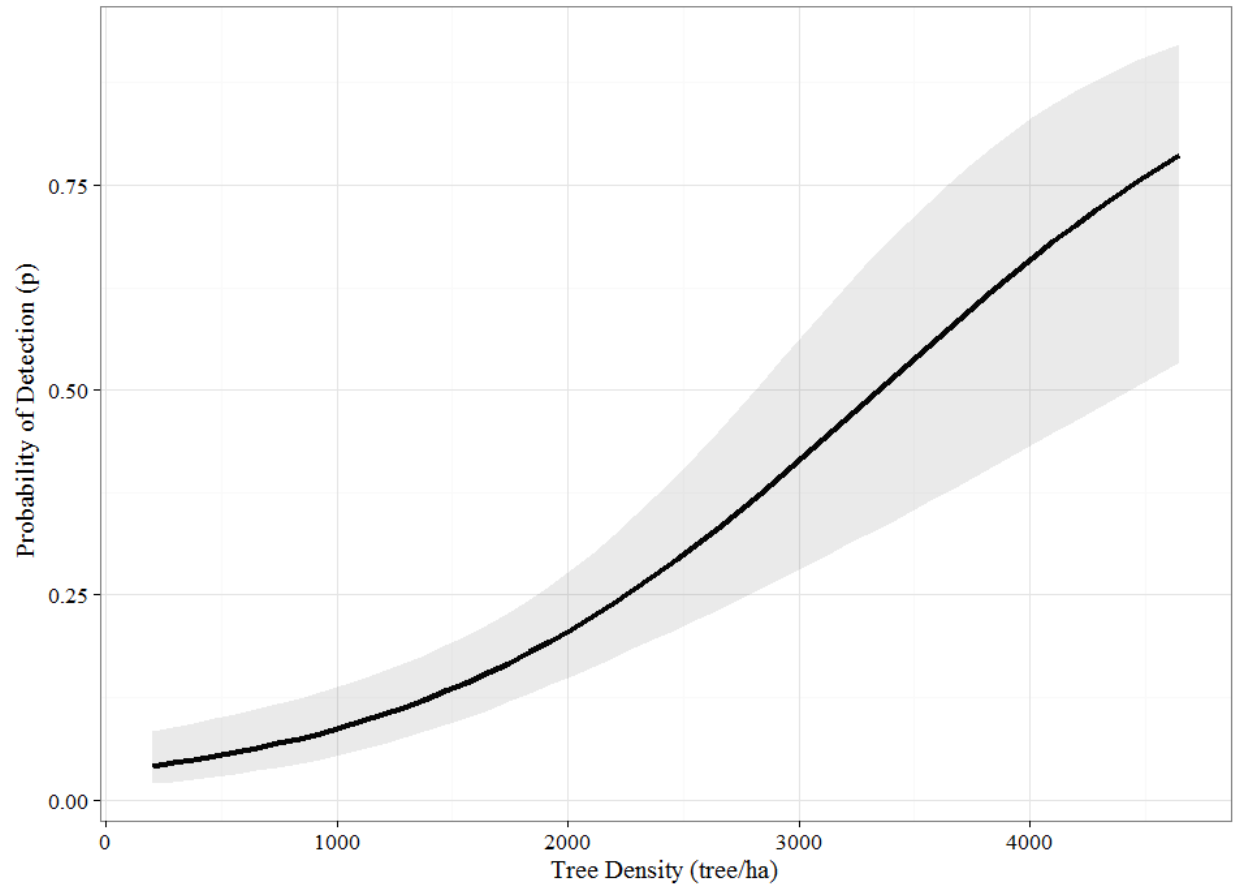


Figure 2-7B Partial effects plot of the relationship between probability of detection of little brown bats (with 95% confidence intervals) and tree density (trees/ha) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

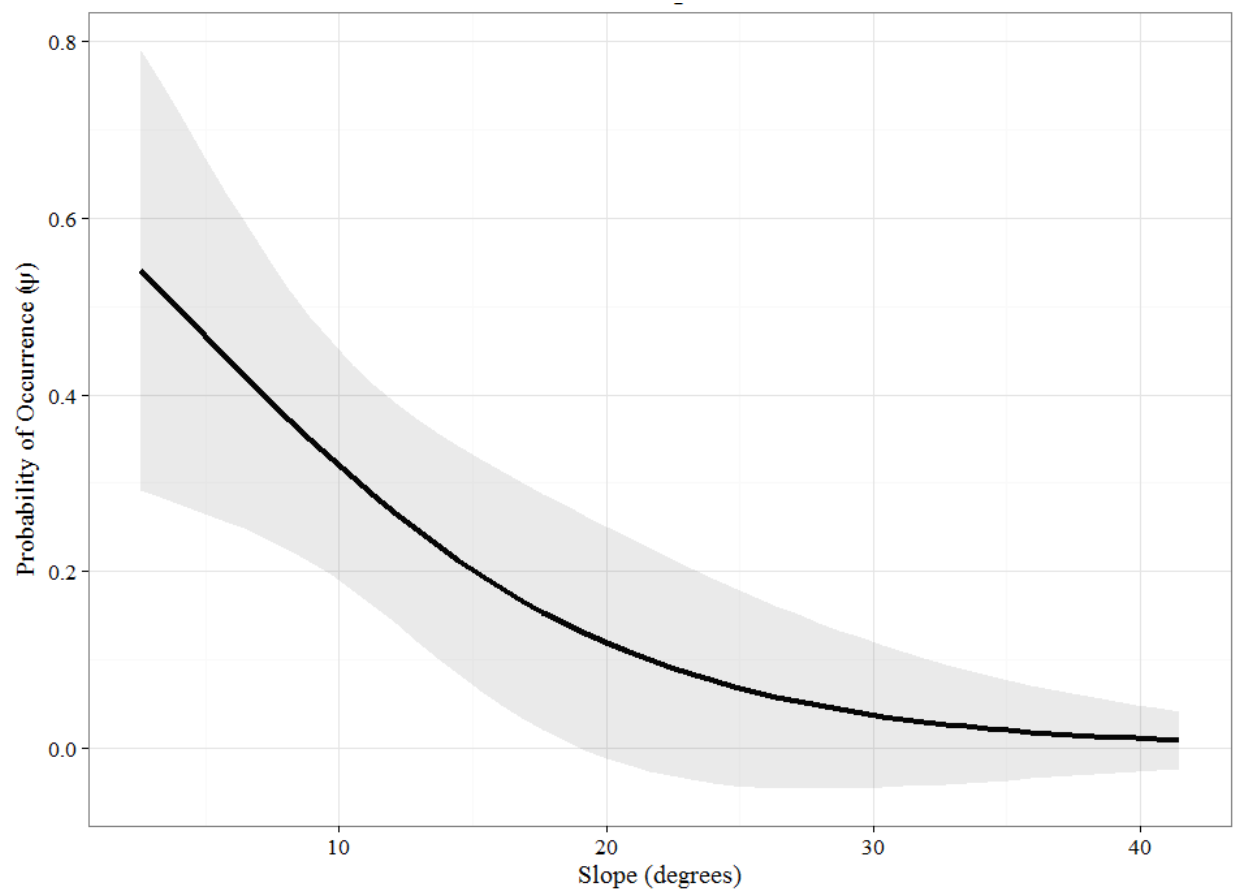


Figure 2-8 Partial effects plot of the relationship between probability of occurrence of northern long-eared bats (with 95% confidence intervals) and slope (degrees) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

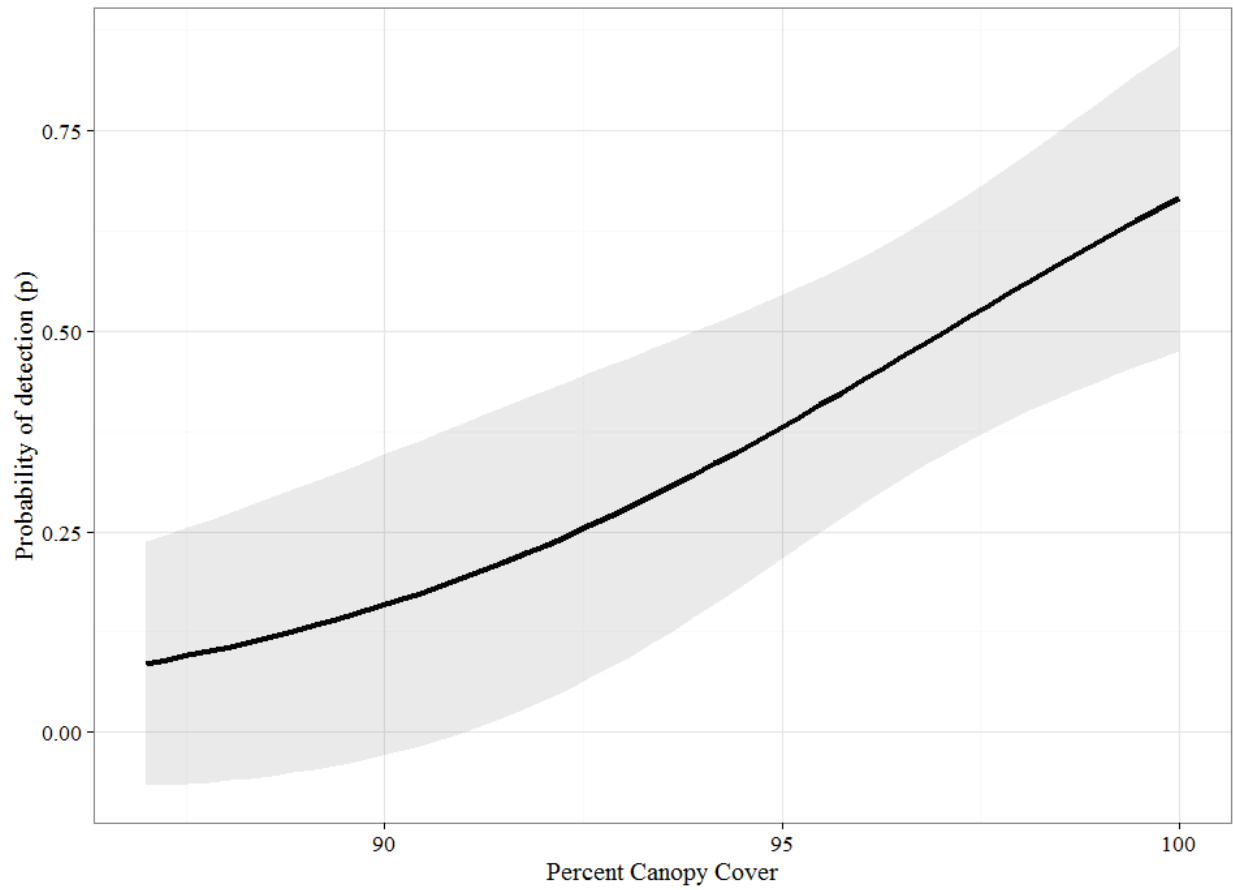


Figure 2-9 Partial effects plot of the relationship between probability of detection of Indiana bats (with 95% confidence intervals) and percent canopy cover at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

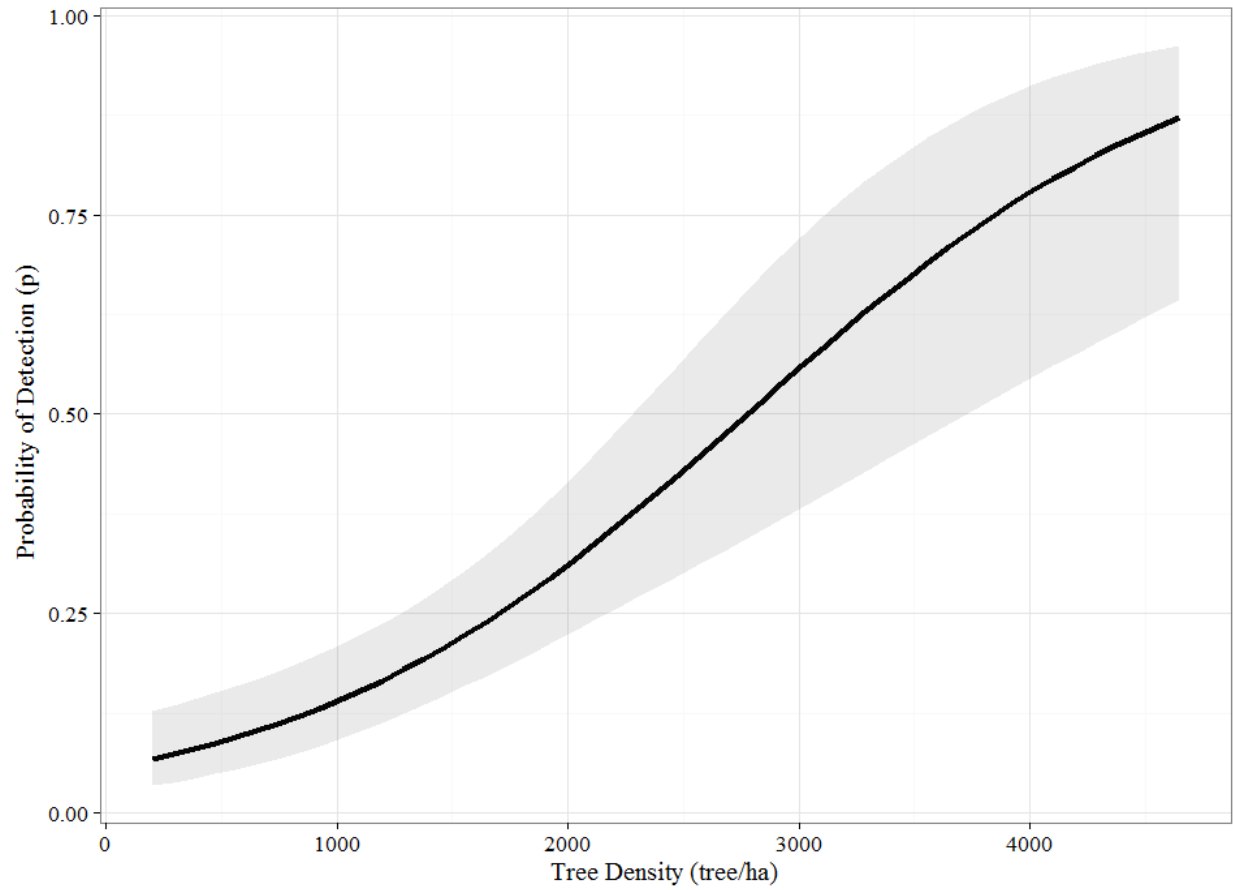


Figure 2-10 Partial effects plot of the relationship between probability of detection of tricolored bats (with 95% confidence intervals) and tree density (trees/ha) at Shenandoah National Park, Virginia, USA, 11 June to 15 August 2015, as identified in the averaged model.

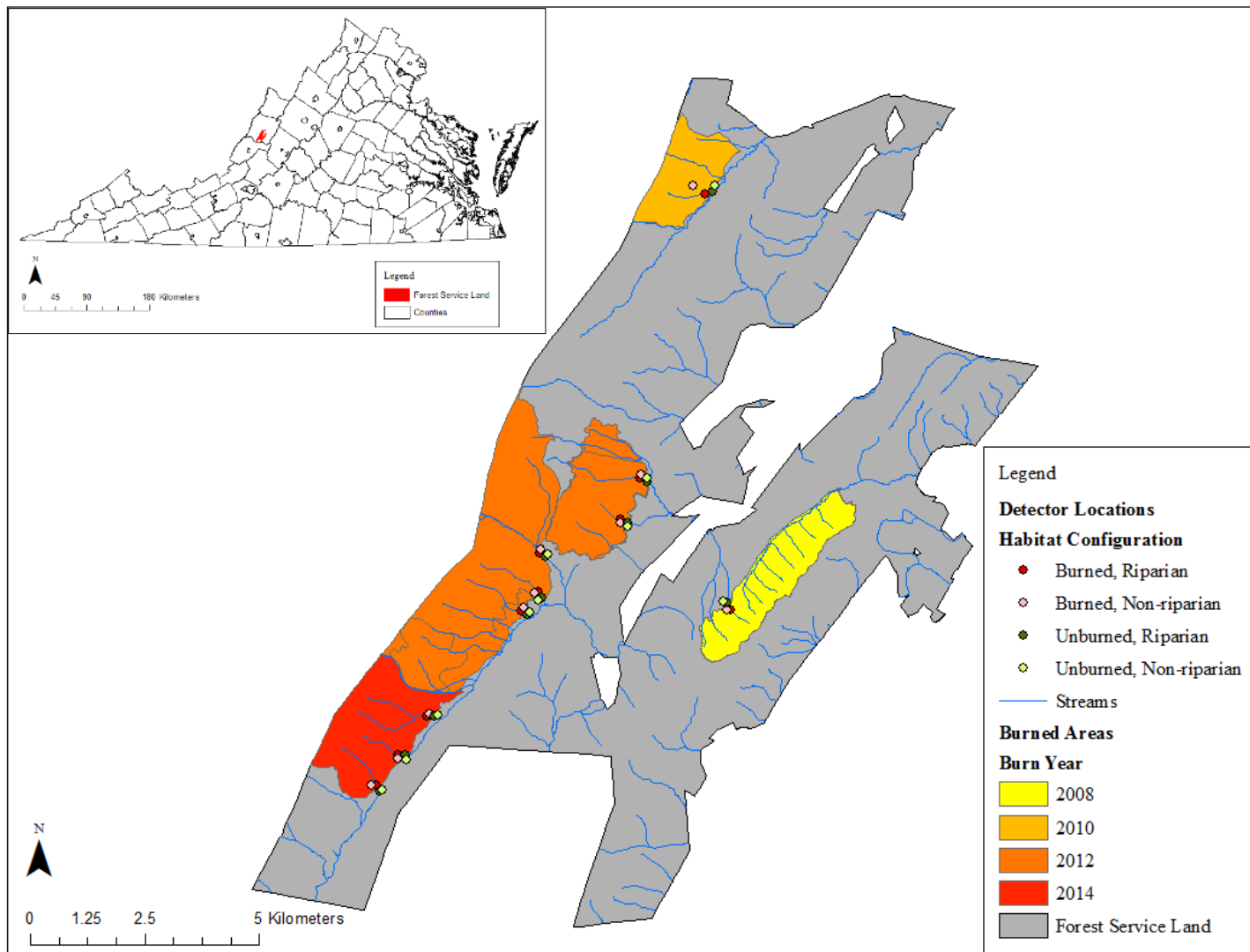


Figure 3-4 Map of bat detector and prescribed burn plot locations on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016.

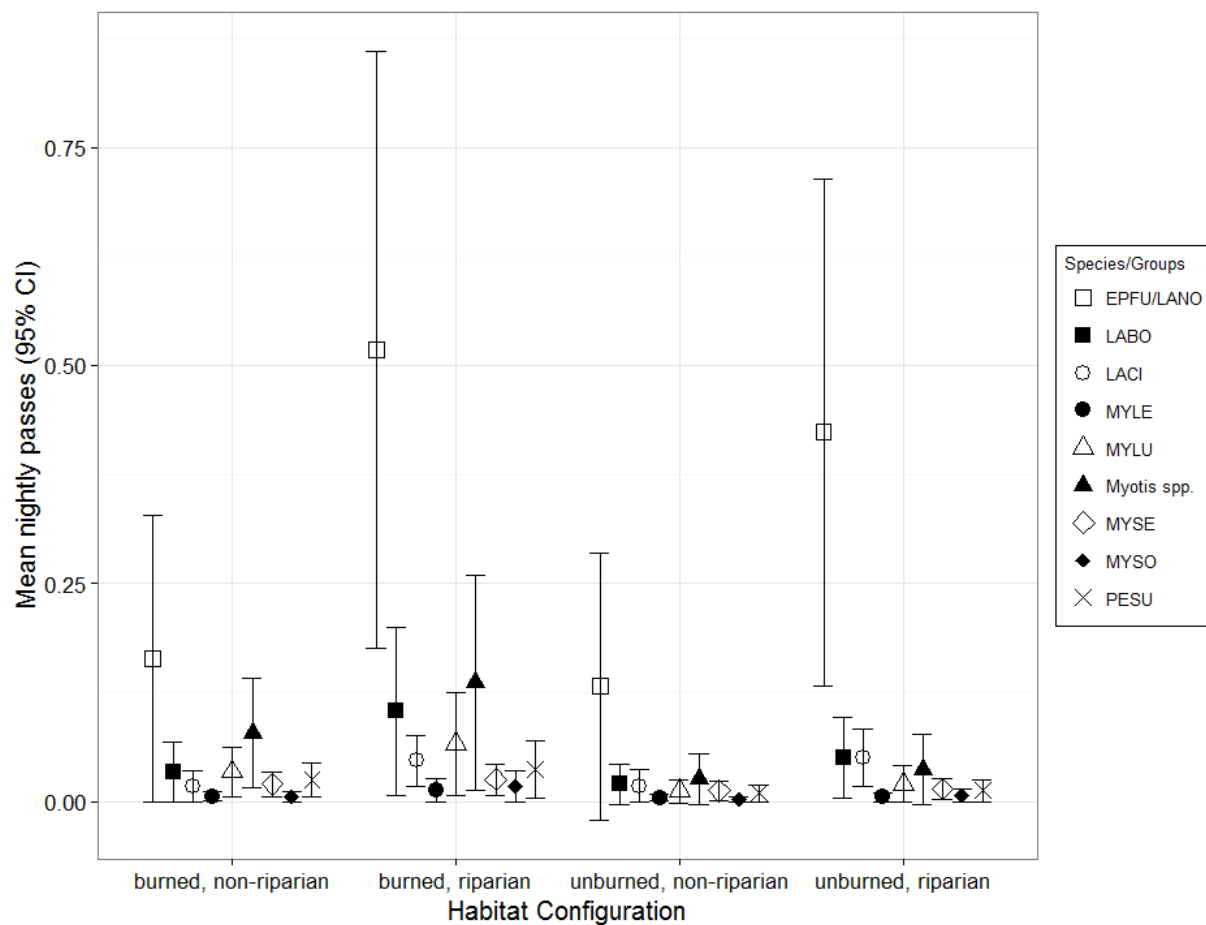


Figure 3-5 Mean nightly passes for bats species and species groups by habitat configuration on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016.

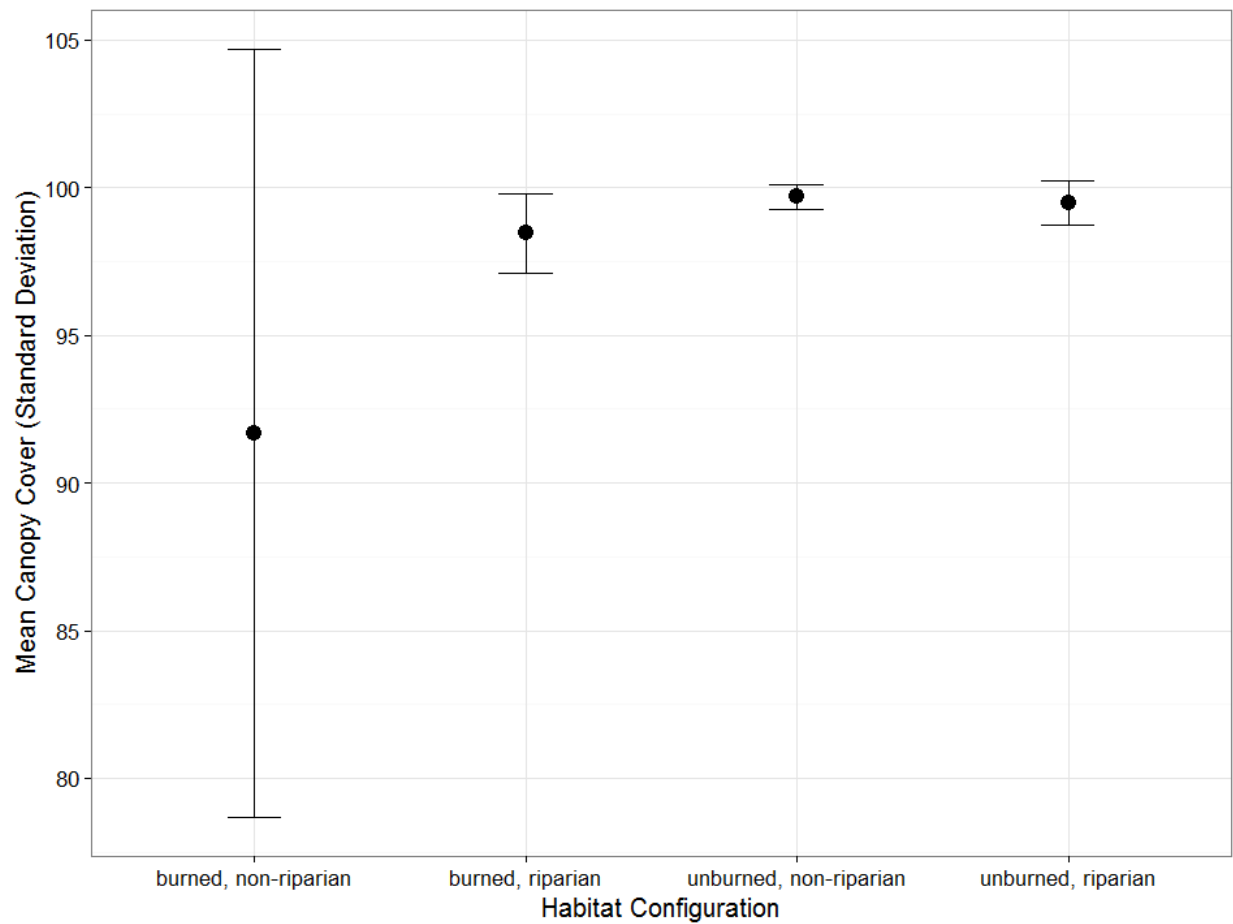


Figure 3-6 Estimates and corresponding standard for multiple linear mixed models exploring the effects of habitat configuration on percent canopy cover on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016.



## Tables

Table 1-1 Models with random effects for site and transect chosen to represent hypotheses about burn and habitat effects on bat activity in the central Appalachians based on literature review.

Model	References
Activity ~ 1 + (1 site/transect)	Null Carter et al., 2000; Loeb and Waldrop, 2008; Silvis et al., 2016
Activity ~ burn condition + (1 site/transect)	
Activity ~ burn condition + aspect + (1 site/transect)	Desta et al., 2004; Flatley et al., 2011
Activity ~ burn condition + elevation + (1 site/transect)	Elliott et al., 1999; Flatley et al., 2011
Activity ~ burn condition + slope + (1 site/transect)	Elliott et al., 1999; Flatley et al., 2011
Activity ~ burn condition + basal area + (1 site/transect)	Arthur et al., 2015; Elliott et al., 1999
Activity ~ burn condition + canopy cover + (1 site/transect)	Arthur et al., 2015
Activity ~ burn condition + burn year + (1 site/transect)	Arthur et al., 2015; Elliott et al., 1999
Activity ~ aspect + (1 site/transect)	Jachowski et al., 2014; Watrous et al., 2006
Activity ~ elevation + (1 site/transect)	Ford et al., 2005
Activity ~ slope + (1 site/transect)	Jachowski et al., 2014; Watrous et al., 2006
Activity ~ basal area + (1 site/transect)	Ford et al., 2005; Owen et al., 2004
Activity ~ canopy cover + (1 site/transect)	Ford et al., 2005
Activity ~ burn condition + aspect + elevation + slope + basal area + canopy cover + burn year + (1 site/transect)	Global

Table 1-2 Competing ( $\Delta\text{QAICc} < 2$ ) negative binomial mixed models describing bat activity, as well as null and global models, with random effects for site and transect, by species, in the Warm Springs Mountain portion of Bath County, Virginia, USA, 24 May to 2 August 2015. We present the degrees of freedom (df), log likelihood (logLik), Akaike's Information Criteria for overdispersion and small sample size (QAICc), delta QAICc (delta), and QAICc weight (weight).

Species	Model(s)	df	logLik	QAICc	$\Delta\text{QAICc}$	weight
<i>Eptesicus fuscus</i> / <i>Lasionycteris noctivagans</i>						
	burn condition + elevation	7	-487.19	154.50	0.00	0.32
	elevation	5	-507.47	155.80	1.28	0.17
	null	4	-522.08	157.70	3.23	0.06
	global	12	-485.62	165.70	11.22	0.00
<i>Lasiurus borealis</i>						
	burn condition + canopy cover	7	-178.37	156.20	0.00	0.22
	burn condition	6	-181.87	156.70	0.49	0.17
	canopy cover	5	-186.05	157.80	1.55	0.10
	burn condition + elevation	7	-180.72	158.10	1.83	0.09
	burn condition + basal area	7	-180.79	158.10	1.88	0.09
	null	4	-190.90	159.40	3.17	0.05
	global	12	-175.53	165.70	9.45	0.00
<i>Lasiurus cinereus</i>						
	canopy cover	5	-162.28	157.30	0.00	0.59
	elevation	5	-164.08	158.90	1.61	0.27
	global	12	-153.67	165.70	8.43	0.01
	null	4	-176.28	167.60	10.31	0.00
<i>Myotis lucifugus</i>						
	burn condition + elevation	7	-179.90	155.70	0.00	0.27
	burn condition	6	-183.09	156.00	0.23	0.24

	null	4	-195.41	161.10	5.35	0.02
	global	12	-177.69	165.70	9.97	0.00
<i>Myotis septentrionalis</i>						
	burn condition + elevation	7	-102.24	161.40	0.00	0.85
	global	12	-97.06	165.70	4.34	0.10
	null	4	-118.95	178.30	16.97	0.00
<i>Myotis sodalis</i>						
	burn condition + elevation	7	-132.29	157.40	0.00	0.75
	null	4	-146.18	165.50	8.12	0.01
	global	12	-129.16	165.70	8.35	0.01
High frequency						
	burn condition + elevation	7	-272.75	155.10	0.00	0.30
	burn condition	6	-278.25	155.70	0.55	0.23
	null	4	-297.53	161.10	5.93	0.02
	global	12	-270.60	165.70	10.58	0.00
Total activity						
	burn condition + elevation	7	-524.61	154.30	0.00	0.29
	elevation	5	-546.64	155.60	1.33	0.15
	burn condition	6	-540.12	156.10	1.82	0.12
	null	4	-560.64	157.10	2.82	0.07
	global	12	-523.54	165.70	11.39	0.00

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Table1-3 Model-averaged coefficients, unconditional standard errors (SE), and 95% upper (UCI) and lower (LCI) confidence intervals for competing ( $\Delta Q A I C c < 2$ ) negative binomial mixed models of bat activity by species in the Warm Springs Mountain portion of Bath County, Virginia, USA, 24 May to 2 August 2015.

Species	Variable	Coefficient	SE	LCI	UCI
<i>Eptesicus fuscus</i> / <i>Lasionycteris noctivagans</i>					
	intercept	0.71	0.42	-0.11	1.54
	burn condition: burn	0.49	0.44	-0.38	1.36
	burn condition: edge	1.89	1.41	-0.88	4.65
	elevation	<b>0.88</b>	<b>0.17</b>	<b>0.55</b>	<b>1.20</b>
<i>Lasiurus borealis</i>					
	intercept	<b>-4.30</b>	<b>0.83</b>	<b>-5.94</b>	<b>-2.64</b>
	burn condition: burn	1.35	0.91	-0.54	3.16
	burn condition: edge	<b>3.68</b>	<b>1.63</b>	<b>0.07</b>	<b>7.00</b>
	canopy cover	-0.41	0.49	-1.41	0.57
	elevation	0.07	0.21	-0.34	0.48
	basal area	-0.07	0.21	-0.48	0.35
<i>Lasiurus cinereus</i>					
	intercept	<b>-1.57</b>	<b>0.31</b>	<b>-2.19</b>	<b>-0.95</b>
	canopy cover	-0.54	0.38	-1.28	0.21
	elevation	0.31	0.49	-0.64	1.27
<i>Myotis lucifugus</i>					
	intercept	<b>-4.19</b>	<b>0.79</b>	<b>-5.75</b>	<b>-2.63</b>
	burn condition: burn	1.23	0.74	-0.24	2.70
	burn condition: edge	<b>4.84</b>	<b>0.96</b>	<b>2.94</b>	<b>6.75</b>
	elevation	0.43	0.47	-0.49	1.35
High frequency bats					
	intercept	<b>-2.30</b>	<b>0.48</b>	<b>-3.26</b>	<b>-1.35</b>
	burn condition: burn	<b>1.26</b>	<b>0.54</b>	<b>0.20</b>	<b>2.33</b>
	burn condition: edge	<b>4.18</b>	<b>0.67</b>	<b>2.86</b>	<b>5.51</b>

Total activity	elevation	0.43	0.41	-0.38	1.23
	intercept	<b>0.86</b>	<b>0.42</b>	<b>0.03</b>	<b>1.73</b>
	burn condition: burn	0.85	0.35	-0.32	1.58
	burn condition: edge	3.04	0.44	-0.52	4.98
	elevation	0.85	0.16	-0.06	1.42

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Table 1-4 Estimates, standard errors (SE), and 95% upper (UCI) and lower (LCI) confidence intervals for the top negative binomial mixed model of bat activity by species in the Warm Springs Mountain portion of Bath County, Virginia, USA, 24 May to 2 August 2015.

Species	Variable	Coefficient	SE	LCI	UCI
<i>Myotis septentrionalis</i>					
	intercept	<b>-5.27</b>	<b>1.03</b>	<b>-7.84</b>	<b>-3.59</b>
	burn condition: burn	<b>2.10</b>	<b>0.98</b>	<b>0.18</b>	<b>4.02</b>
	burn condition: edge	<b>4.99</b>	<b>1.05</b>	<b>3.16</b>	<b>7.49</b>
	elevation	<b>1.26</b>	<b>0.35</b>	<b>0.62</b>	<b>2.04</b>
<i>Myotis sodalis</i>					
	intercept	<b>-5.17</b>	<b>1.04</b>	<b>-7.21</b>	<b>-3.13</b>
	burn condition: burn	1.12	0.93	-0.70	2.94
	burn condition: edge	<b>4.86</b>	<b>1.10</b>	<b>2.70</b>	<b>7.01</b>
	elevation	<b>1.54</b>	<b>0.44</b>	<b>0.68</b>	<b>2.41</b>

Table 1-5 Competing ( $\Delta\text{AICc} < 2$ ) negative binomial mixed models of activity by species, as well as null and global models, with random effects for site and transect in the Warm Springs Mountain portion of Bath County, Virginia, USA, 24 May to 2 August 2015.

Species	Model(s)	df	logLik	AICc	$\Delta\text{AICc}$	weight
<i>Perimyotis subflavus</i>	null	4	-67.73	143.70	0.00	0.17
	burn condition	6	-65.98	144.60	0.81	0.11
	aspect	5	-67.07	144.60	0.82	0.11
	elevation	5	-67.45	145.30	1.57	0.08
	burn condition + aspect	7	-65.29	145.40	1.64	0.08
	burn condition + elevation	7	-65.33	145.50	1.71	0.07
	canopy cover	5	-67.62	145.70	1.91	0.07
	global	12	-63.97	154.20	10.49	0.00

Table 2-1A Detection covariates chosen for foraging habitat models for bat species present in the Central Appalachians based on literature review.

Covariates	References
Canopy cover	Ford et al., 2005
Tree density	O’Keefe et al., 2014
Mean temperature	Britzke et al., 2013; Griffin, 1971
Mean wind speed	Britzke et al., 2013
Precipitation	Britzke et al., 2013



Table 2-1B False-positive (FP) covariates chosen for foraging habitat models for bat species present in the Central Appalachians based on literature review.

Covariates	References
Eastern red bat (LABO)	Britzke et al., 2013, 2011; Clement, 2016; Ford, 2014
Hoary bat (LACI)	Britzke et al., 2013, 2011; Clement, 2016; Ford, 2014
Big brown bat (EPFU)	Britzke et al., 2013, 2011; Clement, 2016; Ford, 2014
Little brown bat (MYLU)	(Britzke et al., 2011, 2013; Clement, 2016; Ford, 2014)
Northern long-eared bat (MYSE)	Britzke et al., 2013, 2011; Clement, 2016; Ford, 2014
Tree density	O’Keefe et al., 2014
Mean wind speed	Britzke et al., 2013
Precipitation	Britzke et al., 2013
Mean Humidity	Britzke et al., 2013; Griffin, 1971

Table 2-1C State covariates chosen for foraging habitat models for bat species present in the Central Appalachians based on literature review.

Covariates	References
Burn condition	Carter et al., 2000; Loeb and Waldrop, 2008; Silvis et al., 2016a
Burn condition + burned*YSB	Armitage and Ober, 2012; Nowacki and Abrams, 2008
Burn condition * Aspect	Buchalski et al., 2013; Mladenoff and Baker, 1999
Burn condition * elevation	Buchalski et al., 2013; Mladenoff and Baker, 1999
Burn condition * slope	Buchalski et al., 2013; Mladenoff and Baker, 1999
Burn condition * tree density	Hutchinson et al., 2005; Loeb and Waldrop, 2008
Elevation	Ford et al., 2005
Slope	D. Jachowski et al., 2014; Watrous et al., 2006
Aspect	D. Jachowski et al., 2014; Watrous et al., 2006
Tree density	Ford et al., 2005; Owen et al., 2004

Table 2-2 Covariates of interest for occupancy, detection, and false-positive detection for bat species in Shenandoah National Park, Virginia, USA 2015.

<b>Variable</b>	<b>Explanation</b>	<b>Units/ Categories</b>
Burn Condition	Whether the site was burn, unburned, or edge habitat.	Categorical: burned, unburned, edge
Burn Size	Number of acres burned in each individual fire.	hectares
Burn Age	Number of years since last burn.	number
Edge Distance	Meters between the acoustic site and fire boundary.	meters
Elevation	Meters above sea level	meters
Slope	Rate of change in elevation measured in degrees.	degrees
Aspect	Direction of the maximum rate of change in slope. Sin transformed.	Sine transformed so that 0 is north, 0.49 is east and west, and 1 is south.
Canopy cover	% of sky covered by over story vegetation	percent
Stem Density	Average number of trees per acre.	Trees per hectare
Little brown bat presence	Whether or not little brown bats are detected at the site.	Categorical: present or absent
Northern long-eared bat presence	Whether or not northern long-eared bats are detected at a site	Categorical: present or absent
Hoary bat presence	Whether or not hoary bats are detected at a site	Categorical: present or absent
Eastern red bat presence	Whether or not eastern red bats are detected at a site	Categorical: present or absent

Table 2-3 Summary of site-level/night-level agreement (out of 71 total sites/ 639 total nights) in species presence between Kaleidoscope and Echoclass for bat species (except hoary bat results which come from Kaleidoscope only) in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. “Present” specifies the number of sites/nights that both Kaleidoscope and Echoclass agreed that each species was present. Absent specifies the number of sites that both Kaleidoscope and Echoclass agreed that a species was absent. Disagree indicates the number of sites that either Echoclass or Kaleidoscope said that a particular species was present but the other program did not.

	PRESENT	ABSENT	DISAGREE
<i>Eptesicus fuscus</i>	17/94	18/370	36/175
<i>Lasiurus cinereus</i>	40/109	31/530	-
<i>Lasiurus borealis</i>	20/32	2/255	49/352
<i>Myotis leibii</i>	1/1	42/530	28/108
<i>Myotis lucifugus</i>	1/3	34/470	36/1
<i>Myotis septentrionalis</i>	15/34	19/429	37/176
<i>Myotis sodalis</i>	7/21	33/491	31/127
<i>Perimyotis subflavus</i>	4/9	38/494	29/136

Table 2-4 Competing ( $\Delta\text{AICc} < 2$ ) models describing bat occupancy by species in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. Occupancy was modeled with false-positive models except for the hoary bat which was modeled with single-season occupancy models. We present the degrees of freedom (df), log likelihood (logLik), Akaike's Information Criteria for small sample size (AICc), delta AICc (delta), and AICc weight (weight).

Species	Detection	FP	State	k	AICc	$\Delta\text{AICc}$	weight	loglik
<i>Eptesicus fuscus</i>								
	tree density	LACI	burn condition + burned*YSB	9	780.17	0.00	0.38	-379.61
	tree density	LACI	burn condition	8	780.86	0.69	0.27	-381.27
	tree density	LACI	1	6	782.76	2.59	0.10	-384.72
<i>Lasiurus borealis</i>								
	wind speed	MYLU	1	6	890.09	0.00	0.39	-438.39
	wind speed	MYLU	slope	7	891.74	1.65	0.17	-437.98
<i>Lasiurus cinereus</i>								
	wind speed	-	burn condition * elevation	8	543.97	0.00	0.18	-262.82
	temperature	-	burn condition * elevation	8	544.79	0.82	0.12	-263.24
	wind speed	-	tree density	4	545.33	1.36	0.09	-268.36
	canopy cover	-	burn condition * elevation	8	545.91	1.94	0.07	-263.79
<i>Myotis leibii</i>								
	temperature	MYLU	slope	7	179.70	0.00	0.63	-81.96
	temperature	MYLU	1	6	183.17	3.47	0.11	-84.93
<i>Myotis lucifugus</i>								
	tree density	MYSE	burn condition*slope	11	441.30	0.00	0.89	-207.42
	tree density	MYSEs	1	6	451.17	9.87	0.01	-218.90
<i>Myotis septentrionalis</i>								
	tree density	MYLU	slope	7	623.37	0.00	0.37	-303.80
	precipitation	MYLU	slope	7	624.44	1.07	0.22	-304.33
	1	MYLU	slope	6	625.22	1.85	0.15	-305.96
	tree density	MYLU	1	6	628.69	5.32	0.03	-307.69
<i>Myotis sodalis</i>								

<i>Perimyotis subflavus</i>	canopy cover	MYLU	1	6	434.73	0.00	0.20	-210.71
	canopy cover	MYLU	elevation	7	434.83	0.09	0.19	-209.52
	canopy cover	MYLU	burn condition*aspect	11	435.41	0.67	0.14	-204.47
	canopy cover	MYLU	aspect	7	435.64	0.90	0.13	-209.93
	canopy cover	MYLU	burn condition	8	435.92	1.18	0.11	-208.80
	canopy cover	MYLU	slope	7	436.00	1.27	0.11	-210.11
<i>Perimyotis subflavus</i>	tree density	MYLU	slope	7	351.86	0.00	0.56	-168.04
	tree density	MYLU	1	6	354.76	2.89	0.13	-170.72

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Table 2-5 Model-averaged coefficients, unconditional standard errors (SE), parameter type, and 95% upper and lower confidence intervals for competing bat occupancy models ( $\Delta\text{AICc} < 2$ ) by species in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the parameter type, coefficient, standard error (SE), and upper and lower confidence intervals (CI).

Species	Covariates	Parameter	Coefficient	SE	Lower CI	Upper CI
<i>Eptesicus fuscus</i>	burn condition: edge	$\Psi$	1.66	1.01	-0.33	3.64
	burn condition: burn	$\Psi$	0.11	0.9	-1.65	1.88
	burn condition: burn*YSB	$\Psi$	-0.78	1.18	-3.09	1.53
	tree density	p	<b>0.74</b>	<b>0.35</b>	<b>0.05</b>	<b>1.42</b>
	hoary bat	fp	<b>3.59</b>	<b>0.31</b>	<b>2.98</b>	<b>4.19</b>
<i>Lasiurus cinereus</i>	burn condition edge*elevation	$\Psi$	-1.56	1.53	-4.56	1.44
	burn condition burn*elevation	$\Psi$	1.15	1.22	-1.24	3.54
	tree density	$\Psi$	0.13	0.32	-0.49	0.75
	wind speed	p	-0.19	0.18	-0.53	0.16
	temperature	p	-0.09	0.17	-0.41	0.23
	canopy cover	p	-0.05	0.12	-0.28	0.18
<i>Lasiurus borealis</i>	slope	$\Psi$	-0.09	0.24	-0.55	0.37
	wind speed	p	<b>-0.28</b>	<b>0.12</b>	<b>-0.51</b>	<b>-0.05</b>
	little brown bat	fp	13.3	48.8	-82.34	108.95
<i>Myotis septentrionalis</i>	slope	$\Psi$	<b>-1.10</b>	<b>0.49</b>	<b>-2.06</b>	<b>-0.14</b>
	tree density	p	0.15	0.18	-0.21	0.51
	precipitation	p	0.17	0.32	-0.45	0.79
	little brown bat	fp	<b>6.05</b>	<b>0.57</b>	<b>4.93</b>	<b>7.17</b>
<i>Myotis sodalis</i>	elevation	$\Psi$	0.17	0.4	-0.6	0.95
	burn condition: edge*aspect	$\Psi$	0.70	1.82	-2.88	4.27

burn condition: burn*aspect	Ψ	0.39	1.14	-1.84	2.63
aspect	Ψ	-0.20	0.94	-2.03	1.64
burn condition: edge	Ψ	0.49	1.18	-1.83	2.81
burn condition: burn	Ψ	0.20	0.92	-1.61	2.00
slope	Ψ	-0.06	0.25	-0.55	0.42
canopy cover	p	<b>0.63</b>	<b>0.25</b>	<b>0.14</b>	<b>1.12</b>
little brown bat	fp	<b>5.19</b>	<b>0.53</b>	<b>4.14</b>	<b>6.23</b>

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Table 2-6 Estimates, standard errors (SE), parameter type, and 95% upper and lower confidence intervals for the top bat occupancy model by species in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the parameter type, coefficient, standard error (SE), and upper and lower confidence intervals (CI).

Species	Covariate	Parameter	Estimate	SE	Lower CI	Upper CI
<i>Myotis leibii</i>						
	slope	$\Psi$	<b>-0.99</b>	<b>0.50</b>	<b>-1.96</b>	<b>-0.02</b>
	temperature	p	<b>1.32</b>	<b>0.59</b>	<b>0.17</b>	<b>2.47</b>
	little brown bat	fp	<b>8.85</b>	<b>1.17</b>	<b>6.55</b>	<b>11.14</b>
<i>Myotis lucifugus</i>						
	burn condition edge	$\Psi$	19.10	30.80	-41.32	79.57
	burn condition burn	$\Psi$	19.20	30.80	-41.19	79.68
	slope	$\Psi$	-37.00	56.70	-148.1	74.13
	burn condition edge*slope	$\Psi$	36.70	56.70	-74.38	147.81
	burn condition burn*slope	$\Psi$	36.30	56.70	-74.75	147.44
	tree density	p	<b>0.91</b>	<b>0.18</b>	<b>0.55</b>	<b>1.27</b>
	northern long-eared bat	fp	<b>5.94</b>	<b>0.58</b>	<b>4.80</b>	<b>7.08</b>
<i>Perimyotis subflavus</i>						
	slope	$\Psi$	-0.83	0.47	-1.75	0.09
	tree density	p	<b>0.93</b>	<b>0.19</b>	<b>0.56</b>	<b>1.31</b>
	little brown bat	fp	<b>8.89</b>	<b>1.18</b>	<b>6.58</b>	<b>11.20</b>

Table 3-1 *A priori* zero-inflated negative binomial mixed models and corresponding hypotheses that incorporate burn and riparian variables to assess effects on bat activity level, Bath County, Virginia, USA, 17 May to 4 August 2016.

<b><i>A priori</i> Models</b>	<b>Literature Cited</b>
Null	Burnham and Anderson, 2002
Burn	Carter et al., 2000; Loeb and Waldrop, 2008; Silvis et al., 2016a
Riparian	Ford et al., 2005; Fukui et al., 2006; Grindal et al., 1999; Monadjem and Reside, 2008; Swystun et al., 2007
Burn + Riparian	Elliott et al., 1999
Burn * Riparian	Elliott et al., 1999

Table 3-2 Model selection results for zero-inflated negative binomial mixed models exploring impacts of burn and riparian conditions, with random effects for site, treatment block, and year since burn (YSB), on bat activity, by species, on the George Washington National Forest, Bath County, Virginia, USA, 17 May to 4 August 2016. We present the degrees of freedom (df), log likelihood (logLik), Akaike's Information Criteria for small sample size (AICc), delta AICc (delta), and AICc weight (weight).

Models by Species	df	logLik	AICc	ΔAICc	weight
<i>Eptesicus fuscus</i> / <i>Lasionycteris noctivagans</i>					
Burn + (1 site) + (1 group)	6	-3069.60	6151.2	0.00	0.46
Burn+Riparian + (1 site) + (1 group)	7	-3069.30	6152.6	1.41	0.23
1 + (1 site) + (1 group)	5	-3071.69	6153.4	2.17	0.16
Burn*Riparian + (1 site) + (1 group)	8	-3069.28	6154.6	3.38	0.09
Riparian + (1 site) + (1 group)	6	-3071.42	6154.9	3.64	0.07
<i>Lasiurus cinereus</i>					
Burn + (1 site) + (1 group)	6	-743.82	1499.7	0.00	0.53
Burn+Riparian + (1 site) + (1 group)	7	-743.76	1501.6	1.89	0.20
1 + (1 site) + (1 group)	5	-746.14	1502.3	2.63	0.14
Burn*Riparian + (1 site) + (1 group)	8	-743.72	1503.5	3.81	0.08
Riparian + (1 site) + (1 group)	6	-746.12	1504.3	4.60	0.05
<i>Lasiurus borealis</i>					
Burn + (1 site) + (1 group)	6	-1381.83	2775.7	0.00	0.28
Burn+Riparian + (1 site) + (1 group)	7	-1380.85	2775.7	0.05	0.28
1 + (1 site) + (1 group)	5	-1383.43	2776.9	1.19	0.16
Riparian + (1 site) + (1 group)	6	-1382.49	2777.0	1.32	0.15
Burn*Riparian + (1 site) + (1 group)	8	-1380.53	2777.1	1.42	0.14
<i>Myotis leibii</i>					
1 + (1 site) + (1 group) + (1 YSB)	6	-376.79	765.6	0.00	0.24
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-373.81	765.7	0.07	0.23
Riparian + (1 site) + (1 group) + (1 YSB)	7	-375.94	765.9	0.31	0.20
Burn + (1 site) + (1 group) + (1 YSB)	7	-376.03	766.1	0.48	0.19
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-375.31	766.7	1.05	0.14

<i>Myotis lucifugus</i>					
Riparian + (1 site) + (1 group) + (1 YSB)	7	-1085.99	2186.0	0.00	0.32
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-1085.10	2186.3	0.23	0.28
1 + (1 site) + (1 group) + (1 YSB)	6	-1087.73	2187.5	1.47	0.15
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-1084.89	2187.8	1.82	0.13
Burn + (1 site) + (1 group) + (1 YSB)	7	-1086.93	2187.9	1.88	0.12
<i>Myotis septentionalis</i>					
1 + (1 site) + (1 group) + (1 YSB)	6	-685.58	1383.2	0.00	0.34
Riparian + (1 site) + (1 group) + (1 YSB)	7	-684.72	1383.5	0.27	0.30
Burn + (1 site) + (1 group) + (1 YSB)	7	-685.36	1384.7	1.55	0.16
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-684.50	1385.1	1.86	0.14
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-684.30	1386.7	3.46	0.06
<i>Myotis sodalis</i>					
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-668.77	1353.6	0.00	0.27
Burn + (1 site) + (1 group) + (1 YSB)	7	-669.86	1353.8	0.16	0.25
Riparian + (1 site) + (1 group) + (1 YSB)	7	-670.14	1354.3	0.72	0.19
1 + (1 site) + (1 group) + (1 YSB)	6	-671.19	1354.4	0.81	0.18
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-668.73	1355.5	1.92	0.10
<i>Perimyotis subflavus</i>					
Riparian + (1 site) + (1 group) + (1 YSB)	7	-1007.88	2029.8	0.00	0.37
1 + (1 site) + (1 group) + (1 YSB)	6	-1009.38	2030.8	0.99	0.22
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-1007.51	2031.1	1.27	0.20
Burn + (1 site) + (1 group) + (1 YSB)	7	-1009.01	2032.1	2.26	0.12
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-1007.22	2032.5	2.70	0.10
<i>Myotis spp.</i>					
Riparian + (1 site) + (1 group) + (1 YSB)	7	-1654.71	3323.5	0.00	0.37
Burn+Riparian + (1 site) + (1 group) + (1 YSB)	8	-1654.09	3324.2	0.77	0.25

1 + (1 site) + (1 group) + (1 YSB)	6	-1656.58	3325.2	1.73	0.15
Burn*Riparian + (1 site) + (1 group) + (1 YSB)	9	-1653.71	3325.5	2.02	0.13
Burn + (1 site) + (1 group) + (1 YSB)	7	-1656.02	3326.1	2.62	0.10
Total Activity					
Burn + (1 site) + (1 group)	5	-4077.33	8164.7	0.00	0.32
1 + (1 site) + (1 group)	4	-4078.70	8165.4	0.73	0.22
Burn+Riparian + (1 site) + (1 group)	6	-4076.70	8165.4	0.75	0.22
Riparian + (1 site) + (1 group)	5	-4078.12	8166.3	1.58	0.15
Burn*Riparian + (1 site) + (1 group)	7	-4076.69	8167.4	2.74	0.08

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Table 3-3 Model-averaged coefficients, unconditional standard errors (SE), and upper and lower confidence intervals (CI) for competing ( $\Delta AIC_c < 4$ ) zero-inflated negative binomial mixed models exploring effects of burn and riparian conditions on bat activity by species, Bath County, Virginia, USA, 17 May to 4 August 2016.

Species	Variables	Coefficient	SE	Lower CI	Upper CI
<i>Eptesicus fuscus</i> / <i>Lasionycteris noctivagans</i>					
	Intercept	<b>-2.09</b>	<b>0.66</b>	<b>-3.39</b>	<b>-0.80</b>
	Burn	1.18	0.92	-0.63	2.99
	Riparian	0.23	0.57	-0.90	1.35
	Burn*Riparian	-0.03	0.42	-0.86	0.80
<i>Lasiurus cinereus</i>					
	Intercept	<b>-4.04</b>	<b>0.47</b>	<b>-4.97</b>	<b>-3.12</b>
	Burn	1.02	0.67	-0.28	2.33
	Riparian	-0.04	0.34	-0.71	0.62
	Burn*Riparian	-0.02	0.31	-0.63	0.59
<i>Lasiurus borealis</i>					
	Intercept	<b>-3.99</b>	<b>0.76</b>	<b>-5.48</b>	<b>-2.50</b>
	Burn	0.91	0.96	-0.97	2.79
	Riparian	0.52	0.83	-1.11	2.16
	Burn*Riparian	0.17	0.71	-1.22	1.56
<i>Myotis leibii</i>					
	Intercept	<b>-5.49</b>	<b>0.81</b>	<b>-7.07</b>	<b>-3.91</b>
	Burn	0.17	0.91	-1.61	1.96
	Riparian	0.22	0.92	-1.58	2.02
	Burn*Riparian	0.61	1.34	-2.01	3.23
<i>Myotis lucifugus</i>					
	Intercept	<b>-4.51</b>	<b>0.85</b>	<b>-6.18</b>	<b>-2.84</b>
	Riparian	1.05	1.00	-0.91	3.01
	Burn	0.50	0.81	-1.10	2.09

<i>Myotis septentrionalis</i>	Burn*Riparian	0.13	0.64	-1.13	1.38
	Intercept	<b>-4.43</b>	<b>0.69</b>	<b>-5.79</b>	<b>-3.08</b>
	Riparian	0.48	0.78	-1.04	2.01
	Burn	0.15	0.57	-0.96	1.27
	Burn*Riparian	0.06	0.45	-0.83	0.95
<i>Myotis sodalis</i>	Intercept	<b>-6.15</b>	<b>1.24</b>	<b>-8.58</b>	<b>-3.71</b>
	Burn	1.02	1.18	-1.29	3.34
	Riparian	0.81	1.11	-1.35	2.98
	Burn*Riparian	0.06	0.66	-1.23	1.35
<i>Perimyotis subflavus</i>	Intercept	<b>-4.72</b>	<b>0.87</b>	<b>-6.42</b>	<b>-3.02</b>
	Riparian	0.95	1.05	-1.10	3.00
	Burn	0.24	0.72	-1.17	1.66
	Riparian*Burn	0.12	0.65	-1.15	1.40
<i>Myotis spp.</i>	Intercept	<b>-3.74</b>	<b>0.82</b>	<b>-5.34</b>	<b>-2.13</b>
	Riparian	1.11	1.03	-0.91	3.14
	Burn	0.33	0.76	-1.16	1.83
	Burn*Riparian	0.18	0.74	-1.27	1.64
All Species	Intercept	<b>-1.52</b>	<b>0.73</b>	<b>-2.95</b>	<b>-0.09</b>
	Burn	0.86	0.94	-0.99	2.70
	Riparian	0.41	0.74	-1.04	1.86
	Burn*Riparian	-0.02	0.46	-0.91	0.88

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**Supplementary Material for Chapter 2: Effects of historic wildfire and prescribed fire on site occupancy of bats in Shenandoah National Park, Virginia, USA**

Table S-1A All false- positive models describing big brown bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
tree density	LACI	1	6	781.45	782.76	0.00	0.76
1	LACI	1	5	786.39	787.31	4.56	0.08
temperature	LACI	1	6	786.15	787.46	4.71	0.07
precipitation	LACI	1	6	787.65	788.96	6.20	0.03
canopy cover	LACI	1	6	788.20	789.51	6.75	0.03
wind speed	LACI	1	6	788.30	789.62	6.86	0.02
tree density	LABO	1	6	911.42	912.74	129.98	0.00
1	LABO	1	5	915.10	916.02	133.27	0.00
temperature	LABO	1	6	915.03	916.34	133.58	0.00
precipitation	LABO	1	6	916.20	917.51	134.75	0.00
canopy cover	LABO	1	6	917.00	918.31	135.55	0.00
wind speed	LABO	1	6	917.09	918.41	135.65	0.00
temperature	wind speed	1	6	938.67	939.99	157.23	0.00
temperature	humidity	1	6	938.90	940.22	157.46	0.00
temperature	1	1	5	940.04	940.96	158.20	0.00
precipitation	wind speed	1	6	940.70	942.02	159.26	0.00
precipitation	humidity	1	6	940.89	942.21	159.45	0.00
precipitation	1	1	5	941.84	942.76	160.00	0.00
canopy cover	wind speed	1	6	941.64	942.95	160.19	0.00
canopy cover	humidity	1	6	941.93	943.24	160.48	0.00
temperature	tree density	1	6	942.02	943.33	160.58	0.00
temperature	precipitation	1	6	942.03	943.35	160.59	0.00



tree density	wind speed	1	6	942.17	943.48	160.73	0.00
tree density	humidity	1	6	942.30	943.61	160.85	0.00
1	wind speed	1	5	943.01	943.93	161.17	0.00
1	humidity	1	5	943.22	944.14	161.38	0.00
tree density	1	1	5	943.23	944.15	161.39	0.00
canopy cover	1	1	5	943.69	944.61	161.86	0.00
wind speed	wind speed	1	6	943.33	944.64	161.88	0.00
1	1	1	4	944.06	944.67	161.91	0.00
wind speed	humidity	1	6	943.68	944.99	162.23	0.00
precipitation	tree density	1	6	943.80	945.11	162.35	0.00
precipitation	precipitation	1	6	943.83	945.15	162.39	0.00
wind speed	1	1	5	945.01	945.94	163.18	0.00
tree density	precipitation	1	6	945.14	946.45	163.70	0.00
tree density	tree density	1	6	945.22	946.54	163.78	0.00
1	precipitation	1	5	946.01	946.93	164.17	0.00
1	tree density	1	5	946.05	946.98	164.22	0.00
canopy cover	precipitation	1	6	945.69	947.00	164.24	0.00
canopy cover	tree density	1	6	945.69	947.00	164.24	0.00
wind speed	tree density	1	6	946.99	948.30	165.54	0.00
wind speed	precipitation	1	6	947.01	948.32	165.56	0.00

Table S-1B: All false- positive models describing big brown bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
tree density	LACI	burn condition+burned:YSB.s	9	777.22	780.17	0.00	0.38
tree density	LACI	burn condition	8	778.54	780.86	0.69	0.27
tree density	LACI	1	6	781.45	782.76	2.59	0.10
tree density	LACI	elevation	7	782.03	783.81	3.64	0.06
tree density	LACI	slope	7	782.39	784.17	4.00	0.05
tree density	LACI	burn condition*tree density	11	780.55	785.03	4.86	0.03
tree density	LACI	tree density	7	783.30	785.08	4.91	0.03
tree density	LACI	aspect	7	783.44	785.21	5.05	0.03
tree density	LACI	burn condition*elevation	11	781.73	786.21	6.04	0.02
tree density	LACI	burn condition*aspect	11	782.62	787.10	6.93	0.01
tree density	LACI	burn condition*slope	11	782.86	787.34	7.17	0.01

Table S-2A All false- positive models describing eastern red bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	False-positive	State	k	AICc	d.AICC	w.AICc
wind speed	MYLU	1	6	890.09	0.00	0.680
1	MYLU	1	5	893.73	3.63	0.111
temperature	MYLU	1	6	894.06	3.97	0.093
canopy cover	MYLU	1	6	895.53	5.43	0.045
tree density	MYLU	1	6	895.97	5.88	0.036
precipitation	MYLU	1	6	896.02	5.93	0.035
wind speed	MYSE	1	6	926.44	36.34	0.000
1	MYSE	1	5	927.83	37.74	0.000
canopy cover	MYSE	1	6	928.57	38.47	0.000
temperature	MYSE	1	6	929.18	39.08	0.000
tree density	MYSE	1	6	930.10	40.01	0.000
precipitation	MYSE	1	6	930.20	40.11	0.000
wind speed	precipitation	1	6	1018.06	127.96	0.000
precipitation	1	1	5	1020.59	130.50	0.000
1	humidity	1	5	1020.92	130.83	0.000
temperature	1	1	5	1021.27	131.18	0.000
1	wind speed	1	5	1021.27	131.18	0.000
tree density	1	1	5	1021.28	131.18	0.000
precipitation	humidity	1	6	1022.64	132.55	0.000
precipitation	wind speed	1	6	1022.96	132.87	0.000
temperature	humidity	1	6	1023.27	133.18	0.000
tree density	humidity	1	6	1023.30	133.20	0.000
temperature	wind speed	1	6	1023.64	133.55	0.000
tree density	wind speed	1	6	1023.65	133.56	0.000
canopy cover	tree density	1	6	1025.34	135.24	0.000

canopy cover	1	1	5	1029.73	139.63	0.000
canopy cover	precipitation	1	6	1032.11	142.02	0.000
canopy cover	wind speed	1	6	1032.11	142.02	0.000
canopy cover	humidity	1	6	1032.39	142.29	0.000
tree density	tree density	1	6	1035.40	145.31	0.000
1	tree density	1	5	1036.04	145.94	0.000
1	1	1	4	1036.32	146.23	0.000
temperature	tree density	1	6	1036.99	146.90	0.000
wind speed	tree density	1	6	1037.06	146.97	0.000
wind speed	1	1	5	1038.07	147.98	0.000
wind speed	humidity	1	6	1038.08	147.99	0.000
1	precipitation	1	5	1038.27	148.18	0.000
temperature	precipitation	1	6	1039.07	148.98	0.000
wind speed	wind speed	1	6	1039.69	149.59	0.000
tree density	precipitation	1	6	1039.95	149.86	0.000
precipitation	precipitation	1	6	1040.66	150.57	0.000
precipitation	tree density	1	6	1061.12	171.03	0.000

Table S-2B All false- positive models describing eastern red bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc	evid.rat
wind speed	MYLU	null	6	888.78	890.09	0.00	0.39	1.00
wind speed	MYLU	slope	7	889.96	891.74	1.65	0.17	2.28
wind speed	MYLU	aspect	7	890.59	892.37	2.27	0.12	3.12
wind speed	MYLU	tree density	7	890.75	892.53	2.43	0.12	3.38
wind speed	MYLU	elevation	7	890.76	892.54	2.44	0.11	3.40
wind speed	MYLU	burn condition	8	892.17	894.49	4.39	0.04	9.00
wind speed	MYLU	burn condition * elevation	11	891.38	895.85	5.76	0.02	17.81
wind speed	MYLU	burn condition * burn year	9	893.86	896.81	6.72	0.01	28.80
wind speed	MYLU	burn condition * slope	11	895.52	900.00	9.90	0.00	141.35
wind speed	MYLU	burn condition * aspect	11	896.10	900.57	10.48	0.00	188.68
wind speed	MYLU	burn condition * tree density	11	896.88	901.36	11.26	0.00	279.15

Table S-3A All regular occupancy models describing hoary bat detection by species in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	State	k	AICc	d.AICc	w.AICc
wind speed	1	3	546.84	0.00	0.47
canopy cover	1	3	547.66	0.82	0.31
temperature	1	3	548.63	1.79	0.19
1	1	2	555.07	8.23	0.01
precipitation	1	3	555.43	8.59	0.01
tree density	1	3	556.73	9.89	0.00

Table S-3B All regular occupancy models describing hoary bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICc), and AICc weight (w.AICc).

Detection	State	k	AICc	d.AICc	w.AICc
wind speed	burn condition*elevation	8	543.97	0.00	0.18
temperature	burn condition*elevation	8	544.79	0.82	0.12
wind speed	tree density	4	545.33	1.36	0.09
canopy cover	burn condition*elevation	8	545.91	1.94	0.07
wind speed	elevation	4	546.06	2.09	0.06
wind speed	burn condition*burn size	8	546.22	2.25	0.06
canopy cover	tree density	4	546.60	2.63	0.05
wind speed	1	3	546.84	2.87	0.04
canopy cover	elevation	4	547.03	3.06	0.04
temperature	elevation	4	547.09	3.12	0.04
temperature	tree density	4	547.12	3.15	0.04
canopy cover	1	3	547.66	3.69	0.03
wind speed	aspect	4	547.82	3.85	0.03
wind speed	slope	4	548.16	4.19	0.02
temperature	1	3	548.63	4.66	0.02
canopy cover	slope	4	548.74	4.77	0.02
canopy cover	burn condition*burn size	8	548.87	4.90	0.02
canopy cover	aspect	4	548.95	4.98	0.01
temperature	burn condition*burn size	8	549.12	5.15	0.01
wind speed	burn condition	5	549.28	5.31	0.01
temperature	aspect	4	549.98	6.01	0.01
temperature	slope	4	550.01	6.04	0.01
canopy cover	burn condition	5	550.15	6.18	0.01
wind speed	burn condition*tree density	8	550.54	6.57	0.01
temperature	burn condition	5	551.19	7.22	0.00
wind speed	burn condition*YSB	8	551.75	7.78	0.00
canopy cover	burn condition*tree density	8	551.84	7.87	0.00
temperature	burn condition*tree density	8	552.43	8.46	0.00
canopy cover	burn condition*YSB	8	552.85	8.89	0.00
temperature	burn condition*YSB	8	553.78	9.81	0.00
canopy cover	burn condition*slope	8	553.95	9.98	0.00
wind speed	burn condition*slope	8	554.02	10.05	0.00
wind speed	burn condition*aspect	8	555.95	11.98	0.00
temperature	burn condition*slope	8	556.05	12.08	0.00
canopy cover	burn condition*aspect	8	556.97	13.00	0.00
temperature	burn condition*aspect	8	558.05	14.08	0.00

Table S-4A All false- positive models describing eastern small-footed bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
temperature	MYLU	1	6	181.86	183.17	0.00	0.52
1	MYLU	1	5	184.27	185.19	2.02	0.19
precipitation	MYLU	1	6	185.39	186.70	3.53	0.09
canopy cover	MYLU	1	6	185.71	187.02	3.85	0.08
tree density	MYLU	1	6	185.83	187.14	3.97	0.07
wind speed	MYLU	1	6	186.22	187.53	4.36	0.06
canopy cover	LABO	1	6	305.69	307.01	123.84	0.00
1	LABO	1	5	311.50	312.42	129.25	0.00
precipitation	LABO	1	6	311.49	312.81	129.64	0.00
temperature	LABO	1	6	312.28	313.59	130.42	0.00
wind speed	LABO	1	6	313.48	314.79	131.62	0.00
tree density	LABO	1	6	313.49	314.80	131.63	0.00
canopy cover	precipitation	1	6	398.63	399.94	216.77	0.00
canopy cover	humidity	1	6	401.24	402.55	219.38	0.00
canopy cover	tree density	1	6	403.03	404.34	221.17	0.00
temperature	precipitation	1	6	403.83	405.15	221.98	0.00
canopy cover	wind speed	1	6	404.38	405.69	222.52	0.00
1	precipitation	1	5	405.32	406.24	223.07	0.00
precipitation	precipitation	1	6	405.24	406.56	223.39	0.00
temperature	humidity	1	6	405.78	407.10	223.93	0.00
temperature	1	1	5	406.46	407.39	224.22	0.00
wind speed	precipitation	1	6	406.40	407.71	224.54	0.00
temperature	wind speed	1	6	406.90	408.21	225.04	0.00
precipitation	humidity	1	6	407.00	408.31	225.14	0.00
1	humidity	1	5	407.40	408.33	225.16	0.00



precipitation	1	1	5	407.67	408.59	225.42	0.00
tree density	precipitation	1	6	407.29	408.61	225.44	0.00
1	1	1	4	408.29	408.90	225.73	0.00
temperature	tree density	1	6	407.73	409.05	225.88	0.00
precipitation	wind speed	1	6	408.09	409.40	226.23	0.00
wind speed	humidity	1	6	408.09	409.41	226.24	0.00
wind speed	1	1	5	408.68	409.60	226.43	0.00
1	wind speed	1	5	408.70	409.62	226.45	0.00
precipitation	tree density	1	6	408.91	410.23	227.06	0.00
1	tree density	1	5	409.39	410.31	227.14	0.00
wind speed	wind speed	1	6	409.07	410.38	227.21	0.00
tree density	humidity	1	6	409.32	410.63	227.46	0.00
tree density	1	1	5	410.12	411.04	227.87	0.00
wind speed	tree density	1	6	410.00	411.32	228.15	0.00
tree density	wind speed	1	6	410.53	411.85	228.68	0.00
tree density	tree density	1	6	411.28	412.59	229.42	0.00
canopy cover	1	1	5	415.10	416.02	232.85	0.00

Table S-4B All false- positive models describing eastern small-footed bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
temperature	MYLU	slope	7	177.92	179.70	0.00	0.63
temperature	MYLU	1	6	181.86	183.17	3.47	0.11
temperature	MYLU	tree density	7	182.43	184.21	4.51	0.07
temperature	MYLU	elevation	7	183.31	185.09	5.39	0.04
temperature	MYLU	burn condition*elevation	11	180.70	185.17	5.47	0.04
temperature	MYLU	burn condition+burned:YSB.s	9	182.51	185.46	5.76	0.04
temperature	MYLU	aspect	7	183.79	185.57	5.87	0.03
temperature	MYLU	burn condition	8	185.06	187.38	7.69	0.01
temperature	MYLU	burn condition*slope	11	182.99	187.47	7.77	0.01
temperature	MYLU	burn condition*tree density	11	184.00	188.48	8.78	0.01
temperature	MYLU	burn condition*aspect	11	190.46	194.94	15.24	0.00

Table S-5A All false- positive models describing little brown bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
tree density	MYSE	1	6	449.86	451.17	0.00	1.00
canopy cover	MYSE	1	6	463.70	465.01	13.84	0.00
1	MYSE	1	5	464.86	465.78	14.61	0.00
temperature	MYSE	1	6	466.73	468.04	16.87	0.00
wind speed	MYSE	1	6	466.83	468.15	16.98	0.00
precipitation	MYSE	1	6	466.85	468.17	17.00	0.00
canopy cover	LABO	1	6	497.95	499.26	48.09	0.00
1	LABO	1	5	502.00	502.92	51.75	0.00
wind speed	LABO	1	6	503.28	504.59	53.42	0.00
temperature	LABO	1	6	503.49	504.80	53.63	0.00
tree density	LABO	1	6	503.73	505.05	53.88	0.00
precipitation	LABO	1	6	504.00	505.31	54.14	0.00
canopy cover	humidity	1	6	584.03	585.34	134.17	0.00
canopy cover	precipitation	1	6	586.99	588.30	137.13	0.00
1	humidity	1	5	589.45	590.38	139.21	0.00
canopy cover	1	1	5	590.06	590.98	139.81	0.00
wind speed	humidity	1	6	590.67	591.99	140.82	0.00
temperature	humidity	1	6	590.90	592.21	141.04	0.00
canopy cover	wind speed	1	6	590.92	592.23	141.06	0.00
tree density	humidity	1	6	591.19	592.50	141.33	0.00
precipitation	humidity	1	6	591.45	592.76	141.59	0.00
1	precipitation	1	5	592.25	593.17	142.00	0.00
canopy cover	tree density	1	6	592.06	593.37	142.20	0.00
wind speed	precipitation	1	6	593.33	594.64	143.47	0.00
temperature	precipitation	1	6	593.64	594.95	143.78	0.00

tree density	precipitation	1	6	593.91	595.23	144.06	0.00
1	1	1	4	594.70	595.30	144.13	0.00
precipitation	precipitation	1	6	594.25	595.56	144.39	0.00
wind speed	1	1	5	595.50	596.43	145.26	0.00
1	wind speed	1	5	595.57	596.49	145.32	0.00
temperature	1	1	5	595.81	596.73	145.56	0.00
tree density	1	1	5	596.36	597.29	146.11	0.00
precipitation	1	1	5	596.68	597.60	146.43	0.00
1	tree density	1	5	596.68	597.60	146.43	0.00
wind speed	wind speed	1	6	596.40	597.71	146.54	0.00
temperature	wind speed	1	6	596.71	598.02	146.85	0.00
tree density	wind speed	1	6	597.23	598.55	147.38	0.00
wind speed	tree density	1	6	597.41	598.72	147.55	0.00
precipitation	wind speed	1	6	597.56	598.87	147.70	0.00
temperature	tree density	1	6	597.81	599.12	147.95	0.00
tree density	tree density	1	6	598.29	599.60	148.43	0.00
precipitation	tree density	1	6	598.66	599.98	148.81	0.00

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Table S-5B All false- positive models describing little brown bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	mn	k	AIC	AICc	d.AICC	w.AICc
tree density	MYSE	burn condition*slope	6	11	436.83	441.30	0.00	0.89
tree density	MYSE	slope	9	7	444.06	445.83	4.53	0.09
tree density	MYSE	1	1	6	449.86	451.17	9.87	0.01
tree density	MYSE	tree density	10	7	451.37	453.15	11.84	0.00
tree density	MYSE	elevation	8	7	451.80	453.57	12.27	0.00
tree density	MYSE	aspect	11	7	451.85	453.63	12.32	0.00
tree density	MYSE	burn condition	2	8	453.75	456.07	14.76	0.00
tree density	MYSE	burn condition*tree density	7	11	451.99	456.46	15.16	0.00
tree density	MYSE	burn condition*elevation	5	11	452.30	456.77	15.47	0.00
tree density	MYSE	burn condition+burned:YSB.s	3	9	455.70	458.65	17.35	0.00
tree density	MYSE	burn condition*aspect	4	11	460.38	464.86	23.55	0.00

Table S-6A All false- positive models describing northern long-eared bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICc	w.AICc
tree density	MYLU	1	6	627.38	628.69	0.00	0.37
precipitation	MYLU	1	6	628.31	629.63	0.93	0.23
1	MYLU	1	5	629.56	630.48	1.79	0.15
canopy cover	MYLU	1	6	629.56	630.88	2.18	0.13
wind speed	MYLU	1	6	630.92	632.23	3.54	0.06
temperature	MYLU	1	6	631.41	632.72	4.03	0.05
canopy cover	LABO	1	6	806.64	807.95	179.26	0.00
1	LABO	1	5	813.77	814.69	186.00	0.00
tree density	LABO	1	6	814.19	815.50	186.81	0.00
temperature	LABO	1	6	815.56	816.87	188.18	0.00
wind speed	LABO	1	6	815.58	816.89	188.20	0.00
precipitation	LABO	1	6	815.58	816.90	188.20	0.00
1	1	1	4	851.50	852.10	223.41	0.00
1	tree density	1	5	852.61	853.54	224.84	0.00
1	precipitation	1	5	853.44	854.37	225.67	0.00
wind speed	1	1	5	853.50	854.42	225.73	0.00
wind speed	wind speed	1	6	854.56	855.87	227.18	0.00
wind speed	tree density	1	6	854.61	855.92	227.23	0.00
temperature	precipitation	1	6	855.10	856.41	227.72	0.00
tree density	precipitation	1	6	855.43	856.75	228.05	0.00
wind speed	precipitation	1	6	855.44	856.76	228.06	0.00
canopy cover	precipitation	1	6	875.74	877.06	248.36	0.00
canopy cover	tree density	1	6	875.85	877.16	248.46	0.00
tree density	tree density	1	6	875.97	877.28	248.59	0.00
canopy cover	humidity	1	6	879.33	880.64	251.95	0.00

canopy cover	wind speed	1	6	883.99	885.31	256.61	0.00
canopy cover	1	1	5	884.68	885.60	256.91	0.00
precipitation	precipitation	1	6	884.57	885.88	257.19	0.00
1	humidity	1	5	887.72	888.64	259.95	0.00
precipitation	tree density	1	6	887.54	888.85	260.16	0.00
tree density	humidity	1	6	888.14	889.45	260.76	0.00
temperature	tree density	1	6	889.00	890.31	261.62	0.00
wind speed	humidity	1	6	889.13	890.44	261.75	0.00
precipitation	humidity	1	6	889.38	890.69	262.00	0.00
temperature	humidity	1	6	889.38	890.69	262.00	0.00
1	wind speed	1	5	892.45	893.38	264.68	0.00
tree density	wind speed	1	6	892.79	894.10	265.41	0.00
tree density	1	1	5	893.41	894.34	265.64	0.00
temperature	wind speed	1	6	894.10	895.41	266.72	0.00
precipitation	wind speed	1	6	894.16	895.47	266.78	0.00
temperature	1	1	5	894.76	895.68	266.99	0.00
precipitation	1	1	5	894.76	895.68	266.99	0.00

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Table S-6B All false- positive models describing northern long-eared bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICc), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICc	w.AICc
tree density	MYLU	slope	7	621.59	623.37	0.00	0.37
precipitation	MYLU	slope	7	622.66	624.44	1.07	0.22
1	MYLU	slope	6	623.91	625.22	1.85	0.15
tree density	MYLU	burn condition*slope	11	622.50	626.97	3.60	0.06
precipitation	MYLU	burn condition*slope	11	623.44	627.92	4.54	0.04
1	MYLU	burn condition*slope	10	624.71	628.37	5.00	0.03
tree density	MYLU	1	6	627.38	628.69	5.32	0.03
precipitation	MYLU	1	6	628.31	629.63	6.25	0.02
tree density	MYLU	elevation	7	628.66	630.44	7.07	0.01
1	MYLU	1	5	629.56	630.48	7.11	0.01
tree density	MYLU	aspect	7	629.15	630.93	7.56	0.01
tree density	MYLU	tree density	7	629.32	631.10	7.73	0.01
precipitation	MYLU	elevation	7	629.52	631.30	7.92	0.01
precipitation	MYLU	aspect	7	630.11	631.88	8.51	0.01
precipitation	MYLU	tree density	7	630.17	631.95	8.58	0.01
1	MYLU	elevation	6	630.72	632.03	8.66	0.00
tree density	MYLU	burn condition	8	629.85	632.18	8.80	0.00
1	MYLU	aspect	6	631.28	632.60	9.22	0.00
1	MYLU	tree density	6	631.42	632.73	9.36	0.00
precipitation	MYLU	burn condition	8	630.75	633.07	9.70	0.00
1	MYLU	burn condition	7	631.94	633.72	10.35	0.00
tree density	MYLU	burn condition+burned:YSB.s	9	631.20	634.15	10.78	0.00
precipitation	MYLU	burn condition+burned:YSB.s	9	631.95	634.90	11.53	0.00
tree density	MYLU	burn condition*elevation	11	630.98	635.46	12.08	0.00
1	MYLU	burn condition+burned:YSB.s	8	633.15	635.47	12.10	0.00



tree density	MYLU	burn condition*tree density	11	633.65	638.12	14.75	0.00
tree density	MYLU	burn condition*aspect	11	633.84	638.32	14.95	0.00
precipitation	MYLU	burn condition*tree density	11	634.62	639.10	15.73	0.00
precipitation	MYLU	burn condition*aspect	11	634.86	639.33	15.96	0.00
1	MYLU	burn condition*aspect	10	636.02	639.69	16.32	0.00
precipitation	MYLU	burn condition*elevation	11	654.17	658.65	35.28	0.00
1	MYLU	burn condition*elevation	10	655.72	659.39	36.02	0.00
1	MYLU	burn condition*tree density	10	658.79	662.45	39.08	0.00

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Table S-7A All false- positive models describing Indiana bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	mn	k	AIC	AICc	d.AICC	w.AICc
canopy cover	MYLU	1	14	6	433.42	434.73	0.00	0.58
wind speed	MYLU	1	17	6	435.98	437.29	2.55	0.16
tree density	MYLU	1	15	6	436.52	437.84	3.10	0.12
1	MYLU	1	13	5	437.63	438.55	3.82	0.09
temperature	MYLU	1	16	6	439.62	440.93	6.20	0.03
precipitation	MYLU	1	18	6	439.63	440.94	6.21	0.03
1	LABO	1	7	5	623.04	623.97	189.23	0.00
tree density	LABO	1	9	6	623.12	624.43	189.70	0.00
temperature	LABO	1	10	6	623.82	625.14	190.40	0.00
canopy cover	LABO	1	8	6	624.88	626.19	191.46	0.00
precipitation	LABO	1	12	6	624.94	626.25	191.52	0.00
wind speed	LABO	1	11	6	625.01	626.32	191.58	0.00
temperature	precipitation	1	34	6	649.29	650.60	215.87	0.00
tree density	precipitation	1	33	6	650.24	651.55	216.81	0.00
canopy cover	1	1	2	5	651.33	652.25	217.52	0.00
1	precipitation	1	31	5	651.46	652.38	217.65	0.00
canopy cover	wind speed	1	26	6	651.32	652.64	217.90	0.00
canopy cover	precipitation	1	32	6	653.06	654.37	219.63	0.00
wind speed	precipitation	1	35	6	653.23	654.54	219.81	0.00
tree density	tree density	1	21	6	700.61	701.93	267.19	0.00
1	humidity	1	37	5	703.36	704.28	269.55	0.00
1	tree density	1	19	5	703.53	704.45	269.72	0.00
tree density	humidity	1	39	6	703.77	705.09	270.35	0.00
precipitation	precipitation	1	36	6	703.85	705.16	270.42	0.00
temperature	humidity	1	40	6	704.95	706.26	271.53	0.00

precipitation	humidity	1	42	6	705.15	706.46	271.73	0.00
wind speed	tree density	1	23	6	705.18	706.50	271.76	0.00
wind speed	humidity	1	41	6	705.20	706.51	271.78	0.00
temperature	tree density	1	22	6	705.32	706.63	271.89	0.00
precipitation	tree density	1	24	6	705.34	706.65	271.91	0.00
canopy cover	humidity	1	38	6	705.35	706.67	271.93	0.00
canopy cover	tree density	1	20	6	705.53	706.84	272.11	0.00
1	1	1	1	4	707.60	708.20	273.47	0.00
tree density	1	1	3	5	707.75	708.67	273.94	0.00
1	wind speed	1	25	5	707.86	708.79	274.05	0.00
tree density	wind speed	1	27	6	708.11	709.42	274.69	0.00
wind speed	1	1	5	5	709.03	709.96	275.22	0.00
temperature	1	1	4	5	709.25	710.17	275.44	0.00
precipitation	1	1	6	5	709.31	710.23	275.50	0.00
wind speed	wind speed	1	29	6	709.29	710.60	275.86	0.00
temperature	wind speed	1	28	6	709.52	710.84	276.10	0.00
precipitation	wind speed	1	30	6	709.56	710.88	276.14	0.00

Table S-7B All false- positive models describing Indiana bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
canopy cover	MYLU	1	6	433.42	434.73	0.00	0.20
canopy cover	MYLU	elevation	7	433.05	434.83	0.09	0.19
canopy cover	MYLU	burn condition*aspect	11	430.93	435.41	0.67	0.14
canopy cover	MYLU	aspect	7	433.86	435.64	0.90	0.13
canopy cover	MYLU	burn condition	8	433.60	435.92	1.18	0.11
canopy cover	MYLU	slope	7	434.23	436.00	1.27	0.11
canopy cover	MYLU	tree density	7	435.14	436.92	2.18	0.07
canopy cover	MYLU	burn condition+burned:YSB.s	9	435.49	438.44	3.70	0.03
canopy cover	MYLU	burn condition*elevation	11	435.47	439.95	5.21	0.01
canopy cover	MYLU	burn condition*slope	11	437.29	441.77	7.03	0.01
canopy cover	MYLU	burn condition*tree density	11	438.01	442.48	7.75	0.00

Table S-8A All false- positive models describing tricolored bat detection and false-positive detection in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
tree density	MYLU	1	6	353.44	354.76	0.00	1.00
canopy cover	MYLU	1	6	375.91	377.22	22.47	0.00
precipitation	MYLU	1	6	376.95	378.27	23.51	0.00
temperature	MYLU	1	6	382.61	383.93	29.17	0.00
1	MYLU	1	5	383.27	384.20	29.44	0.00
wind speed	MYLU	1	6	383.06	384.37	29.61	0.00
tree density	wind speed	1	6	512.01	513.32	158.57	0.00
canopy cover	wind speed	1	6	512.24	513.55	158.79	0.00
canopy cover	LABO	1	6	519.38	520.69	165.93	0.00
tree density	LABO	1	6	519.82	521.13	166.38	0.00
tree density	tree density	1	6	524.09	525.41	170.65	0.00
precipitation	LABO	1	6	525.60	526.91	172.15	0.00
temperature	LABO	1	6	530.34	531.65	176.89	0.00
wind speed	LABO	1	6	532.83	534.15	179.39	0.00
1	LABO	1	5	533.88	534.81	180.05	0.00
canopy cover	precipitation	1	6	602.47	603.78	249.02	0.00
tree density	precipitation	1	6	604.39	605.71	250.95	0.00
canopy cover	humidity	1	6	605.71	607.02	252.26	0.00
canopy cover	tree density	1	6	606.40	607.72	252.96	0.00
tree density	1	1	5	607.05	607.98	253.22	0.00
tree density	humidity	1	6	606.71	608.02	253.26	0.00
precipitation	precipitation	1	6	607.68	609.00	254.24	0.00
canopy cover	1	1	5	608.48	609.40	254.64	0.00
precipitation	humidity	1	6	611.92	613.23	258.47	0.00
precipitation	1	1	5	613.57	614.50	259.74	0.00

precipitation	tree density	1	6	613.83	615.14	260.38	0.00
precipitation	wind speed	1	6	614.58	615.90	261.14	0.00
temperature	precipitation	1	6	615.50	616.82	262.06	0.00
wind speed	precipitation	1	6	615.85	617.17	262.41	0.00
1	precipitation	1	5	616.91	617.83	263.07	0.00
temperature	humidity	1	6	617.95	619.26	264.50	0.00
wind speed	humidity	1	6	618.24	619.56	264.80	0.00
temperature	1	1	5	618.94	619.86	265.11	0.00
wind speed	1	1	5	619.09	620.01	265.25	0.00
1	humidity	1	5	619.45	620.38	265.62	0.00
temperature	tree density	1	6	619.28	620.60	265.84	0.00
wind speed	tree density	1	6	619.63	620.94	266.19	0.00
1	1	1	4	620.72	621.33	266.57	0.00
temperature	wind speed	1	6	620.17	621.48	266.73	0.00
wind speed	wind speed	1	6	620.23	621.54	266.78	0.00
1	tree density	1	5	620.84	621.76	267.00	0.00
1	wind speed	1	5	621.92	622.84	268.09	0.00

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Table S-8B: All false- positive models describing tricolored bat occupancy in Shenandoah National Park, Virginia, USA, 11 June to 2 August 2015. We present the number of parameters (k), Akaike's Information Criteria for small sample size (AICc), delta AICc (d.AICC), and AICc weight (w.AICc).

Detection	FP	State	k	AIC	AICc	d.AICC	w.AICc
tree density	MYLU	slope	7	350.09	351.86	0.00	0.56
tree density	MYLU	1	6	353.44	354.76	2.89	0.13
tree density	MYLU	tree density	7	354.06	355.84	3.97	0.08
tree density	MYLU	burn condition	8	353.85	356.17	4.30	0.06
tree density	MYLU	burn condition + burned:YSB.s	9	354.09	357.04	5.18	0.04
tree density	MYLU	burn condition*tree density	11	352.64	357.11	5.25	0.04
tree density	MYLU	elevation	7	355.35	357.13	5.26	0.04
tree density	MYLU	aspect	7	355.36	357.13	5.27	0.04
tree density	MYLU	burn condition*slope	11	356.34	360.82	8.95	0.01
tree density	MYLU	burn condition*elevation	11	357.97	362.44	10.58	0.00
tree density	MYLU	burn condition*aspect	11	358.41	362.89	11.02	0.00